

**CULTIVAR DIFFERENCES IN
MACRO-ELEMENT NUTRITION OF
BARLEY (HORDEUM VULGARE L.) AS
INFLUENCED BY MINERAL SUPPLY,
TEMPERATURE AND PLANT AGE**

HARALD PERBY



DEPARTMENT OF PLANT PHYSIOLOGY

UNIVERSITY OF LUND, SWEDEN

LUND 1986



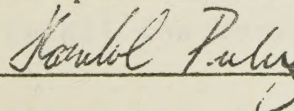
Digitized by the Internet Archive
in 2026

https://archive.org/details/IA41546727_0050

Organization LUND UNIVERSITY Department of Plant Physiology P.O. Box 7007, S-220 07 Lund Sweden		Document name DOCTORAL DISSERTATION	
		Date of issue May 1986	
		CODEN: LUNBDS/(NBFB-1017)/1-16/1986	
Author(s) Harald Perby		Sponsoring organization	
Title and subtitle Cultivar differences in macro-element nutrition of barley (<i>Hordeum vulgare</i> L.) as influenced by mineral supply, temperature and plant age			
Abstract Cultivar differences, mainly in N and K ⁺ nutrition of barley (<i>Hordeum vulgare</i> L.), which was grown in water culture, were investigated, although differences in Ca ²⁺ , Mg ²⁺ , P and S nutrition were also included. Most cultivars were adapted to cultivation in Scandinavia. Cultivar differences in macro-element nutrition were influenced by mineral supply, temperature, plant age and earliness. Variation in seed content of macro-elements were of minor importance for cultivar differences in growth and macro-element accumulation in later stages. Differences in root size of seedlings were usually not related to cultivar differences in total influx of Rb ⁺ (⁸⁶ Rb). In all cases examined, influx of ¹⁵ NO ₃ ⁻ and Rb ⁺ (⁸⁶ Rb) and accumulation of macro-elements differed among cultivars. The relationship between variation in influx of ¹⁵ NO ₃ ⁻ and Rb ⁺ (⁸⁶ Rb) and ability to accumulate N and K ⁺ is complex, partly due to cultivar differences in the pattern of changes occurring in net uptake during ageing. Cultivar differences in partitioning and use-efficiency of N increased during ageing. The N supply has drastic effects on tillering, and consequently on partitioning of dry matter and N. Tillers and main stems compete for previously absorbed ¹⁵ N and their relative competitive strength is related to their accumulation of biomass. Inhibition of tillering during N stress obviates internal competition for a limiting resource. A cultivar with low N requirement produced fewer, but in average larger tillers than a cultivar with a higher N requirement. The cultivars differed also in net retranslocation of ¹⁵ N between main stems and tillers. The implications of these results for practical screening of properties in macro-element nutrition are discussed.			
Key words Barley, calcium, cultivar variation, growth temperature, macro-element, magnesium, mineral supply, nitrate influx, nitrogen, nitrogen retranslocation, partitioning, potassium, rubidium influx, tiller, use-efficiency			
Classification system and/or index terms (if any)			
Supplementary bibliographical information			Language English
ISSN and key title			ISBN
Recipient's notes	Number of pages 16	Price	
	Security classification		

Distribution by (name and address) Harald Perby, Dept of Plant Physiology, P.O. Box 7007, S-220 07 Lund, Sweden

I, the undersigned, being the copyright owner of the abstract of the above-mentioned dissertation, hereby grant to all reference sources permission to publish and disseminate the abstract of the above-mentioned dissertation.

Signature 

Date 18 April 1986

„Segðu mér það, Alvis,
- ölt um rök fira
vörumk, dvergur, að ritir -
hve það sáð heitir,
er sá alda synir,
heimi hverjum í?“

„Bygg heitir með mönnum,
en harr með goðum,
kalla vört vanir,
æti jötnar,
álfar lagastaf,
kalla í helju knipin.“

(Thór said:)

Tell me, Alvis
for all wights' fate
I deem that, dwarf, thou knowest
how the seed is hight
which is sowed by men
in all the worlds so wide?

(Alvis said:)

Tis hight 'Barley' among men,
but 'Breadstuff' among gods;
call the Vanir it 'Well-Grown',
the etins, 'Eating',
the alf-kin, 'Grain'
the wights of Hel, 'Hanging'

**Cultivar differences in macro-element nutrition
of barley (*Hordeum vulgare* L.) as influenced by
mineral supply, temperature and plant age**

Doctoral dissertation

by

Harald Perby

Department of Plant Physiology

University of Lund, Sweden

Doctoral dissertation by due permission of the Faculty of
Science of the University of Lund to be defended in
public at the Department of Plant Physiology on 24 May
1986, at 10.00 am, for the degree of Doctor of Philosophy

Opponent: Dr Lázló Erdei, Szeged, Hungary

Lund 1986

Coden: LUNBDS/(NBFB-1017)/1-16/1986

Table of contents	Page
1. List of papers included in the thesis	3
2. Summary of papers I to VI	4
2.1 Purpose	4
2.2 Experimental procedure	4
2.3 Factors contributing to cultivar differences	5
in uptake and utilization of macro-elements	
2.3.1 Mineral supply and growth temperature	5
2.3.2 Content of minerals in seeds	6
2.3.3 Root size	6
2.3.4 Content of minerals: influx and efflux	7
2.3.5 Partitioning: root-shoot transport and	8
retranslocation	
2.3.6 Use-efficiency	9
2.3.7 Growth rate: shoot size and structure	10
3. Practical implications	10
4. References	12
5. Tables	14
6. Acknowledgements	16
7. Papers I to VI	

1. List of papers included in the thesis:

- I. Perby, H. & Jensén, P. 1983. Varietal differences in uptake and utilization of nitrogen and other macro-elements in seedlings of barley, *Hordeum vulgare*. - *Physiol. Plant.* 58:223-230.
- II. Perby, H. & Jensén, P. 1984. Net uptake and partitioning of nitrogen and potassium in cultivars of barley during ageing. - *Physiol. Plant.* 61:559-565.
- III. Jensén, P. & Perby, H. 1986. Growth and accumulation of N, K⁺, Ca²⁺ and Mg²⁺ in barley exposed to various nutrient regimes and root/shoot temperatures. - *Physiol. Plant.* (In press).
- IV. Perby, H. & Jensén, P. 1986. Variation in growth and accumulation of N, K⁺, Ca²⁺ and Mg²⁺ among barley cultivars exposed to various nutrient regimes and root/shoot temperatures. - *Physiol. Plant.* (In press).
- Va. Perby, H. & Jensén, P. 1986. Vegetative adaptation to N stress regimes in two barley cultivars with different N requirement. - *Plant Soil.* (In press).

Preliminary manuscripts:

- Vb. Perby, H. & Jensén, P. 1986. Tiller expansion and net fluxes of nitrogen among main stems, tillers and roots of two barley cultivars.
- VI. Perby, H. 1986. Cultivar differences in nitrate influx among seedlings of barley grown at two different nitrate concentrations.

References to these papers are in this summary indicated by the corresponding Roman numerals.

2. Summary of papers I to VI

2.1 Purpose

The aim of this thesis has been to study cultivar differences in macro-element nutrition in spring barley. The expression "macro-element nutrition" covers all physiological processes and properties that affect the uptake and utilization of macro-elements. This summary focuses mainly on the following:

- a/ To what extent does cultivar variation in certain endogenous factors contribute to cultivar differences in macro-element nutrition?
- b/ How do mineral supply, temperature and plant age modify the cultivar differences in macro-element nutrition?

2.2 Experimental procedure

The experiments were carried out with different cultivars of spring barley (*Hordeum vulgare* L.) grown in aerated nutrient media (I to VI) or in pots (II) and placed in climate chambers (I to IV, VI) or greenhouse (II, Va,b). All experiments were done with intact plants. N was given as NO_3^- and in some cases as $^{15}\text{NO}_3^-$ (II, Va,b, VI). Content of N was determined with a modified Kjeldahl technique (III). Uptake of NO_3^- was determined by optical ^{15}N analysis; or together with K^+ uptake with ion selective electrodes (II). K^+ , Ca^{2+} and Mg^{2+} were determined by atomic absorption spectrophotometry. Phosphate was determined according to Bertram and van Herk as given by Lindemann (1958) and modified as in I. Radioactivity (^{86}Rb , ^{35}S and ^{32}P) was analyzed by liquid

scintillation spectrometry.

2.3. Factors contributing to cultivar differences in uptake and utilization of macro-elements

2.3.1. Mineral supply and growth temperature

Most important for growth and mineral content was the mineral supply (a standard medium or dilutions), followed by the temperature (III). Third in rank was the choice of cultivar.

The nutrient supply before and after the 'establishment' phase (Briggs 1978) have notable effects on the development of barley plants (II, Va). A restricted N supply during the first 16 days delayed the appearance of individual leaves and decreased the total number of leaves and tillers as well as dry matter and N accumulation in two cultivars of barley (Va).

There are important differences in short- and long-term effects of mineral supply and root temperature on growth and mineral nutrition. Influx of Rb^+ (^{86}Rb) is inhibited in plants with high K^+ levels in roots (references in III). Rb^+ (^{86}Rb) influx per unit root fresh weight is higher in roots adapted to 10°C than in roots adapted to temperatures around 20 to 25°C . In the long run, growth and accumulation of minerals are depressed by restricted mineral supply and low root temperature. However, there is no effect of the root temperature on mineral levels that could explain the reduction in growth.

The cultivation conditions were found to influence cultivar differences in macro-element nutrition (I, IV).

When cultivated for one week in a standard medium, Salve and Birgitta produced more and Edda II and Ingrid less dry matter than 13 other barley cultivars studied (I). When the seedlings were grown in the same medium diluted ten times, the dry weights of Salve and Birgitta were significantly reduced, while the effects were small in the cases of Edda II and Ingrid. In the diluted medium, Edda II and Ingrid performed just as well as most other cultivars. When grown with the combination of low mineral supply and low root temperature, the 19th century land race Nürnberg II, accumulated more dry matter and more N than the modern cultivar Salve (IV). Otherwise Salve performed better.

2.3.2. Content of minerals in seeds

Differences in cultivation of the mother plants or genetic differences cause variation in seed content of minerals in barley. The variation in seed content of N might cause transitional differences in dry weight accumulation (data and references in I). Cultivar differences in N nutrition among older plants are not found to be related to the variation in minerals of seeds (based on data from experiments shown in II and Va). Stress caused by delayed supply of other minerals has no effect on early seedling growth (Dale 1972).

2.3.3. Root size

There are considerable differences in fresh and dry weights of roots among barley cultivars (I, IV, Va). However, differences in influx of $^{15}\text{NO}_3^-$, Rb^+ (^{86}Rb), ^{35}S -sulphate and ^{32}P -phosphate into roots of one-, two- and

three-week-old plants of various barley cultivars correspond only in 8 cases out of 32 to similar differences in root fresh weight (Tab. 1). This indicates that cultivar differences in root size are of limited importance for cultivar differences in macro-element absorption in up to three-week-old plants grown in water culture.

2.3.4. Content of minerals: influx and efflux

Cultivar differences in total contents of macro-elements were found in all cases examined (Tab. 2). They change during ageing, according to differences in earliness of the cultivars (II, IV). The differences are modified by the mineral supply and the cultivation temperature (I, II, IV, VI). Cultivar differences in N content were larger among barley seedlings grown in a standard medium for one week than among seedlings grown in the same medium diluted ten times (I). The high-lysine line Sv 73 608 seems to be more sensitive to the combination of high-salt conditions and a relatively low root temperature than its almost isogenic mother line Mona (IV).

Most studies of cultivar differences in ion influx into the roots focus on K^+ or Rb^+ (references in VI). Such differences have also been shown for $^{15}NO_3^-$, ^{35}S -sulphate and ^{32}P -phosphate influx into roots of one-week-old barley plants (VI; Pettersson 1978; P. Jensén, personal communication). In the case of $^{15}NO_3^-$ influx, the NO_3^- supply before the uptake experiment influenced the differences among the cultivars (VI). Nürnberg II, a 19th century land race, belonged to the highest ranked group when grown in a medium with 2 mM NO_3^- , and to the

lowest ranked group when grown in a medium with 10 mM NO_3^- .

For one-, two- and three-week-old barley plants exposed to various combinations of mineral supply and differential root/shoot temperature, there were no significant relations between Rb^+ (^{86}Rb) influx and K^+ content (IV). For $^{15}\text{NO}_3^-$ influx into one-week-old seedlings the situation was partly different (VI). This lack of a general significant correlation between influx and contents of specific elements at a certain growth stage can be explained by cultivar differences in efflux and by changes in the uptake systems during ageing (II, IV). Three stages could be distinguished when net uptake of NO_3^- and K^+ by barley plants grown in water culture was followed during 85 days (II): 1) A low net ion uptake by seedlings; 2) an increasing net uptake during a period with rapid vegetative development; 3) a steady decline in net ion uptake in older stages. The timing of these three stages of net uptake of NO_3^- and K^+ differed between Bonus and Hellas. Similarly, the differences in daily net uptake of NO_3^- and K^+ between these two cultivars changed during ageing.

2.3.5. Partitioning: root-shoot transport and retranslocation

For barley plants up to three weeks of age the cultivar differences in root-shoot partitioning of N were smaller than the differences in root-shoot partitioning of K^+ , Mg^{2+} , Ca^{2+} , P and S (I, IV). The root-shoot partitioning did not change when six-day-old seedlings of barley were

transferred to a N free medium for nine days (I). Similarly, the cultivar differences in root-shoot transport of ^{15}N were small among one-week-old seedlings of barley (VI). For older plants, differences in tillering between cultivars Kajsa and Hellas were closely related to differences in partitioning of dry matter and N (Va). The N supply strongly influenced the partitioning of N between main stems and tillers. Among grain-filling barley plants, there were cultivar differences in partitioning of N and K^+ and recently supplied ^{15}N and K^+ (^{86}Rb) among leaves, senescent leaves, ears and stems (II). Changes in partitioning during ageing were influenced by the earliness of the cultivars.

There is a considerable retranslocation of N in barley plants (Vb). The rate of net translocation of ^{15}N from main stems to tillers differs between cultivars Hellas and Kajsa. Tillers and main stems compete for N, and their relative competitive strengths are related to their accumulation of biomass.

2.3.6. Use-efficiency

In I to IV a standard medium or dilutions were used. The reduced growth rate of plants supplied with diluted media could be explained by the limited N supply. The cultivar differences in levels of other elements obtained in these experiments is of limited importance. Differences in levels of N (or its inverted value: use-efficiency ratio) among one-week-old seedlings are comparatively small. Larger differences in levels of N were

recorded among older plants (IV, Va). The difference in dry weight production between cultivars Hellas and Kajsa could partly be explained as differences in N use-efficiency (Va). For snapbean, tomato and alfalfa, cultivar differences in ability to grow well on small amounts of specific elements are connected to genetic differences in use-efficiency of these elements (Gabelman and Gerloff 1982). Differences in use-efficiency reflect variation in biochemistry or subcellular compartmentation of the element (Memon et al. 1985).

2.3.7. Growth rate: shoot size and structure

The N supply strongly influences the development of barley (Va). The plants adjust their growth rate, mainly by regulation of tillering. Thereby they also adjust their future need for N. Kajsa grew better than Hellas at most N regimes (Va). Kajsa produced fewer, but on an average larger tillers than Hellas. During N stress Kajsa also inhibited tiller expansion more efficiently than Hellas (Va).

3. Practical implications

From the above discussion it can be concluded that cultivar differences in macro-element nutrition are caused by genetic variation in many physiological processes. The relative importance of the individual factors varies. Differences in some of the parameters, like seed content of macro-elements and root size, are of limited importance for the total variation. Factors such as total content of macro-elements and use-efficiency seem to be more important. For influx of ions and partitio-

ning of dry matter and elements, the differences obtained changed during ageing. The cultivar differences in most factors studied in this thesis are modified by the mineral supply and the growth temperature.

These observations indicate that four conditions must be fulfilled when cultivars of barley are screened for differences in mineral nutrition:

- a. The methods used must selectively isolate such genetic differences in endogenous factors that contribute to cultivar variation in macro-element nutrition.
- b. The plants must be cultivated so that their phenotypes resemble those of plants grown in the field.
- c. Variation due to differences in earliness must be compensated for (II).
- d. The observed cultivar differences must be qualitatively reliable on a long-term basis.

When a large number of cultivars are screened simultaneously, a fifth condition has to be fulfilled:

- e. Measurements must be relatively simple to make.

The application of these criteria limits the number of parameters that are worth comparing in applied selection programs. Detailed comparisons of branching patterns in roots and of efflux and retranslocation of ions in a large number of cultivars are too laborious. Comparisons of responses of accumulation and use-efficiency of specific macro-elements, and in growth rate, dry matter production and tillering pattern to mineral stress are reasonably reliable and relatively simple to do.

In addition to the factors discussed in this thesis cultivar differences in ability to form associations with microorganisms might be important (Azcón and Ocampo 1981, Ela et al. 1982).

4. References

- Azcón, R. & Ocampo, J.A. 1981. Factors affecting the vesicular-arbuscular infection and mycorrhizal dependency of thirteen wheat cultivars. - *New Phytol.* 87:677-685.
- Briggs, D.E. 1978. *Barley*. - Chapman and Hall Ltd, London. p. 225. ISBN 0-412-11870-X.
- Dale, J.E. 1972. Growth and photosynthesis in the first leaf of barley. The effect of time of application of nitrogen. - *Ann. Bot.* 36: 967-979.
- Ela, S.W., Anderson, M.A. & Brill, W. J. 1982. Screening and selection of maize to enhance associative bacterial nitrogen fixation. - *Plant Physiol.* 1564-1567.
- Gabelman, W.H. & Gerloff, G.C. 1982. The search for, and interpretation of, genetic controls that enhance plant growth under deficiency levels of a macronutrient. - In *Genetic Specificity of Mineral Nutrition in Plants* (M.R. Sarič, ed.), pp. 301-312. The Serbian Academy of Sciences and Arts, Belgrade.
- Lindemann, W. 1958. Observation on the behaviour of phosphate compounds in *Chlorella* at the transition from dark to light. - In *Proceedings of the 2nd International Conference of the Peaceful Uses of Atomic Energy* 24:8-15.
- Memon, A.R., Saccomani, M. & Glass, A.D.M. 1985. Effi-

- ciency of potassium utilization by barley varieties:
The role of subcellular compartmentation. - J. Exp.
Bot. 36:1860-1876.
- Pettersson, S. 1978. Varietal differences in rubidium
uptake efficiency of barley roots. - Physiol. Plant.
44:1-6.
- Snedecor, G.W & Cochran, W.G. 1974. Statistical Methods.
- The Iowa State University Press, Ames IA. pp. 172-
198, 557. ISBN 0-8318-1560-6.

5. Tables

Tab. 1. The relation between root fresh weight and influx per root of $^{15}\text{NO}_3^-$, $\text{Rb}^+(\text{}^{86}\text{Rb})$, ^{35}S -sulphate and ^{32}P -phosphate. The roots were exposed to isotope-labelled media for 1 h and then rinsed for 10 min in inactive medium with the same composition. U refers to unpublished data (P. Jensen, personal communication). The number (n) of cultivars included in each experiment is given. Symbols for treatments refer to VI ($^{15}\text{NO}_3^-$) or III (other isotopes). Levels of significance are indicated by stars: * $0.05 > P > 0.01$, ** $P < 0.01$; ns = not significant (Snedecor and Cochran 1974).

Element	Data from	n	Treat- ment	Plant age (days)		
				6 or 7	14	21
$^{15}\text{NO}_3^-$	VI	6	2 mM KNO_3 10 mM KNO_3	*		
				ns		
$\text{Rb}^+(\text{}^{86}\text{Rb})$	III,	6	I	ns	ns	ns
	IV		II	ns	ns	ns
			III	*	*	ns
			IV	ns	**	ns
	U	12	I	ns		
	U	12	I	ns		
^{35}S - sulphate	U	6	I	*	ns	ns
			II	ns	*	ns
			III	ns	ns	**
			IV	ns	**	ns
	U	11	I	ns		
	U	12	I	ns		
	U	14	I	ns		
^{32}P - phosphate	U	14	I	ns		

Tab. 2. Cultivar differences in total contents of macro-elements in barley reported in I, II, IV, Va and VI. Values for S and P do not include fractions from seeds. + indicates that cultivar differences have been shown. Empty space: no study conducted. Growth stages (Briggs 1978): E = "establishment" (seedling); GPG = "the grand period of growth"; GF = grain-filling.

Element	Paper	Growth stage		
		E	GPG	GF
N	I	+		
	II			+
	IV	+	+	
	Va		+	
	VI	+		
K	I	+		
	II		+	+
	IV	+	+	
Ca, Mg	I	+		
	IV	+	+	
P, S	I	+		

6. Acknowledgements

During my doctoral studies I have received valuable and encouraging support, both scientific and moral, from my supervisor, Dr Paul Jensén.

Dr Janet Bornman corrected the language in this summary and gave together with Prof. Anders Kylin and Dr Tomas Lundborg valuable comments on the preliminary versions.

Agne Gustafsson struggled with the duplicator and finally succeeded in printing this thesis. He was assisted by Eva Glantz.

I am also greatly indebted to Karin Andersson, Inga Rydén and Dr Patrick Meurling.

The investigations received generous financial support from the Swedish Council for Forestry and Agricultural Research, O.E. and Edla Johanssons Foundation, The Swedish Society for the Conservation of Nature, Hierta-Retzius' Foundation, P.O. Lundells Foundation and the Royal Physiographical Society, Lund.

Varietal differences in uptake and utilization of nitrogen and other macro-elements in seedlings of barley, *Hordeum vulgare*

Harald Perby and Paul Jensén

Perby, H. and Jensén, P. 1983. Varietal differences in uptake and utilization of nitrogen and other macro-elements in seedlings of barley, *Hordeum vulgare*. — *Physiol. Plant.* 58: 223–230.

Growth and uptake of N, P, S, K, Ca and Mg in barley (*Hordeum vulgare* L.) were studied in water culture using young plants of 17 cultivars. Large varietal differences were obtained in dry weight production and mineral accumulation. The differences were not the same for plants grown in high- and low-salt media. For plants grown under both conditions there was a good correlation between dry weight production and total N content. Total shoot contents of K and Ca were closely correlated with shoot dry weight. Utilization of P and S in high- and low-salt plants and Mg in low-salt plants was variable in relation to dry weight production in both types of nutrient conditions. The correlation between dry weight and total content of Mg in high-salt plants was good. These differences in mineral economy between young barley plants were partly caused by varietal differences in relative growth rate, and in high-salt seedlings also by differences in seed content of N. The significance of root size, and of uptake, root-shoot partitioning and use-efficiency of specific elements differed; all four factors were important for P and S, but had varying impact on K, Mg and Ca. For N, differences in root size and ion accumulation were the most important factors causing varietal variation in mineral nutrition. — In a special experiment seedlings of barley were transferred to N-free nutrient solution after six days of adequate N supply. There was no significant varietal differences in use-efficiency ratio of N. Root/shoot partitioning of N was unaffected.

Additional key words — Low-salt plants, high-salt plants, phosphorus, potassium, sulfur, calcium, magnesium.

H. Perby (reprint requests) and P. Jensén, Dept. of Plant Physiology, Univ. of Lund, Box 7007, S-220 07 Lund, Sweden.

Introduction

In many plant species important inherited differences in mineral nutrition have been shown between varieties (see reviews and books by Gerloff 1963, Vose 1963, Epstein and Jefferies 1964, Epstein 1972, Läuchli 1976, Wright 1976, Clark and Brown 1980, Clarkson and Hanson 1980, Clark 1982, Saric 1982). The variation is due to genetically controlled differences (Epstein 1972) in size and morphology of the roots (Hackett 1968), demand for mineral elements caused by differences in relative growth rate (Chapin and Bielecki 1982), and in uptake (influx and efflux), transport (Pettersson 1978, Doddema and Telkamp 1979, Glass

and Perley 1980, Jensén and Pettersson 1980, Glass et al. 1981), and in use-efficiency of specific elements (Gerloff 1976, Whiteaker et al. 1976). In some cases the linkage between genetic and physiological variation is known (Gabelman 1976, Gabelman and Gerloff 1982).

Several investigators have tried to develop screening techniques that would allow selection of cultivars with desirable qualities in mineral nutrition by as simple means as possible (Wright 1976, Glass et al. 1981) and the present study is an analysis of patterns of mineral nutrition among seedlings of 17 cultivars of barley. Each of the parameters mentioned above, except root morphology, was examined. The relative contribution

Received 27 January, 1983; revised 15 March, 1983

of each to the total variation in mineral nutrition among cultivars was investigated. Most of the cultivars selected for the experiments are adapted to cultivation in Scandinavian regions.

Abbreviations – RGR, relative growth rate, SD, standard deviation.

Materials and methods

Seeds of barley [*Hordeum vulgare* L., cvs Salve, Risø 1508, Kajså (earlier Sv 67 529), Birgitta, Bonus, Kristina, Nürnberg II, Mona, Eva, Alva, Tellus, Hellas, Gunilla, Cilla, Sv 78 460, Edda II and Ingrid] were soaked and germinated in darkness on moist filter paper in petri dishes at 22°C. After three days, the seedlings were inserted through holes drilled through round plastic discs (35 mm in diameter). Three plant groups, each containing ten seedlings, were placed together in 2 l black-painted glass beakers containing 1.8 l aerated nutrient solution. Water losses from the beakers were replaced daily with distilled water.

Plants were grown in climate chambers at 25 ± 1°C, relative humidity of ca 50% and under continuous light (irradiance ca 25 W m⁻², General Electric F48 power groove 17 CVX fluorescent lamps). The design of the experiments and composition of the nutrient solutions are summarized in Fig. 1.

In experiments A and B half the material in each plant group was digested in a 2:1 mixture of concentrated HNO₃ and HClO₄. Contents of K, Mg and Ca in plants and K and Mg in seeds were determined by atomic absorption spectrophotometry (Perkin-Elmer 403). The net uptake of S and P in plants (labelled as

³⁵S-sulfate and ³²P-phosphate) was determined by liquid scintillation spectrophotometry. P determinations in seeds were done according to the method of Bertram and van Herk as given by Lindemann (1958), modified by replacement of hydrazine sulfate with ascorbic acid. The rest of the material was ground and used for determination of total N content, using a Kjeldahl technique adapted to automatic digestion and distillation (Tecator Kjeltec System 1003).

Results

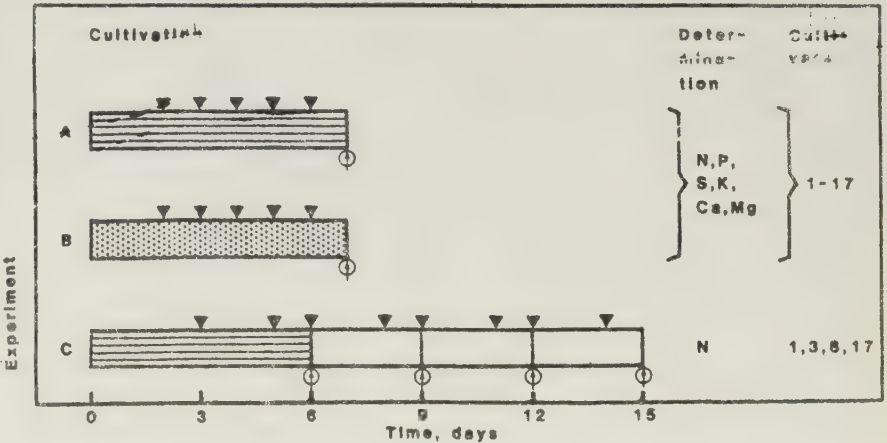
Seeds

Dry weights and total contents of N, P, K and Mg varied among seeds of different cultivars of barley (Tab. 1). The total content of mineral elements in seeds was much less than total amounts found in the seven-day-old seedlings of the cultivars (Tab. 1, Figs 2B, 3A and B

Tab. 1. Average dry weights and contents of four mineral elements in ten seeds of 17 cultivars of barley. Computed from contents in three lots of 100 mixed and ground seeds each per cultivar.

Parameter	Mean ± SD	Range		Unit
		Upper limit	Lower limit	
Dry weight	0.42±0.05	0.50	0.29	g
Nitrogen	0.54±0.06	0.66	0.43	mmol
Phosphorus	0.055±0.010	0.069	0.039	mmol
Potassium	0.044±0.008	0.056	0.030	mmol
Magnesium	0.019±0.003	0.025	0.014	mmol

Fig. 1. Design of experiments. Fresh and dry weights of shoots and roots were determined in all experiments. Cultivars are indicated by numbers (see Fig. 2). Hatched area indicates cultivation in high salt medium (2.0 mM KNO₃, 1.0 mM Ca(NO₃)₂, 1.0 mM MgSO₄, 1.0 mM KH₂PO₄, 0.5 mM Na₂ HPO₄, 0.2 mM Fe-EDTA, 0.5 µM MnSO₄ and 1.5 µM H₃BO₃), dotted area, cultivation in low-salt medium (composed as the high-salt medium, but diluted ten times), and white area, cultivation in nitrogen-free nutrient solution (composed as the high-salt medium, but nitrate replaced by equimolar amounts of chloride). Black triangles indicate changes of nutrient solution, and circles with arrows mark harvest of three plant groups of each cultivar. Nutrient solutions used in experiments A and B were labelled with ³²P-phosphate and ³⁵S-sulfate.



and 4A and C), whereas difference in dry weights of seeds and seedlings was small.

Comparison of high- and low-salt seedlings

Both fresh and dry weights of the shoots varied among the cultivars (Fig. 2A and B), but were generally higher for plants cultivated in the high-salt medium. On the contrary, fresh weights of roots were higher for plants cultivated in the low-salt medium. Differences between dry weights of roots of high- and low-salt plants of each cultivar were generally insignificant. 'Salve' (cultivar No. 1, see Fig. 2) and 'Birgitta' (cv. 4) had the highest shoot dry weights in both experiments, although the dry weight of their shoots was lower when grown on low-salt medium. Dry weights of shoots of 'Edda II' (cv. 16) and 'Ingrid' (cv. 17) were low and about the same under both culture conditions.

Total content of N and net uptake of P and S were higher in shoots and roots of high-salt plants than in low-salt plants (Fig. 3A–C). Significant differences in anion levels among the cultivars were observed for both high- and low-salt-plants, especially in the shoots. Total anion content or net uptake was always highest in high-salt plants of 'Salve' (cv. 1). In contrast, 'Ingrid' (cv. 17), had low P and S uptake and the lowest total N content of the cultivars in experiment A (Fig. 3A–C).

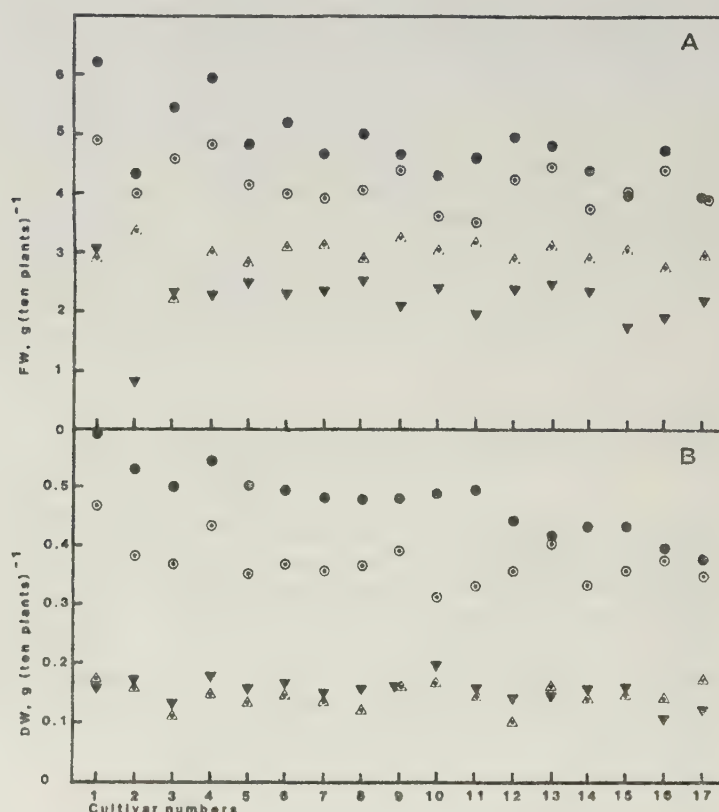
In general, shoots of high- and low-salt plants of each cultivar differed less in total content of cations (Fig. 4A–C) than in elements supplied as anions. For many cultivars higher total contents of Mg and K were found in the low-salt than in high-salt shoots. A lower content of N in the high-salt plants was correlated with a smaller difference in N-content between high- and low-salt plants. The same was true for content of cations and uptake of P. Although 'Salve' had the highest total content or net uptake of all elements in the high-salt plants, the mineral level in the seeds of 'Salve' was not exceptionally high (data not shown).

A significant correlation (Snedecor and Cochran 1974) was found between total content of nitrogen and potassium in high-salt-shoots ($\text{mmol K} = 0.45 \times \text{mmol N} - 0.02 \text{ mmol}$, $r = 0.87$, $P < 0.01$), but not in low-salt shoots. When a correlation analysis was made between dry weight and N-content of roots and shoots, respectively, r was higher for shoots (Tab. 2). Dry weights and total mineral contents were more closely correlated in high- than in low-salt plants.

Effect of sudden nitrogen shortage

The plants continued to grow after transfer to N-free nutrient solution (Fig. 5) but showed decreased internal concentration of N in shoots and roots (Fig. 6). Total N

Fig. 2. Fresh (A) and dry (B) weights for seven-day-old barley seedlings of 17 cultivars. Shoots (filled circles) and roots (filled triangles) of ten seedlings grown in high-salt medium, and of shoots (unfilled circles) and roots (unfilled triangles) of ten seedlings grown in low-salt medium. Cultivars are indicated by numbers: (1) Salve, (2) Risø 1508, (3) Kajsa (earlier Sv 67 529), (4) Birgitta, (5) Bonus, (6) Kristina, (7) Nürnberg II, (8) Mona, (9) Eva, (10) Alva, (11) Tellus, (12) Hellas, (13) Gunilla, (14) Cilla, (15) Sv 78460, (16) Edda II, and (17) Ingrid. Values are means of three replicates. SE usually less than 7%.



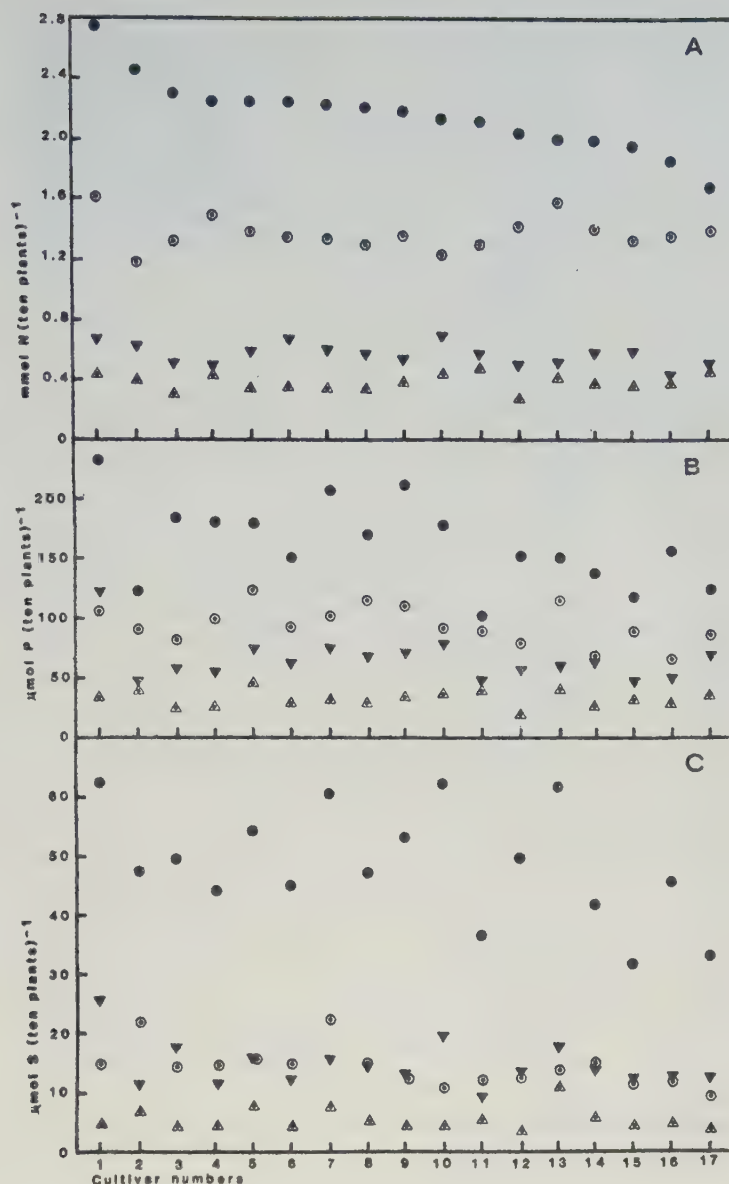


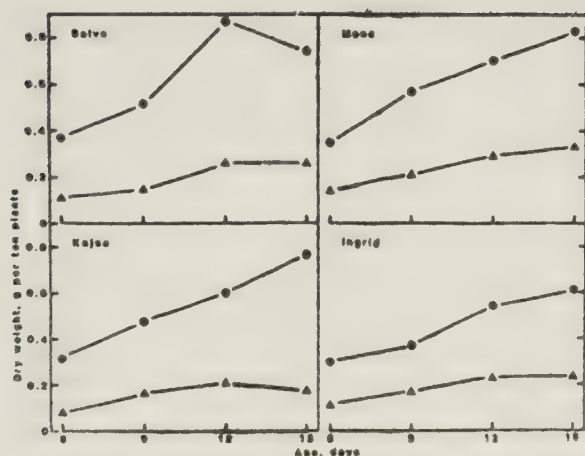
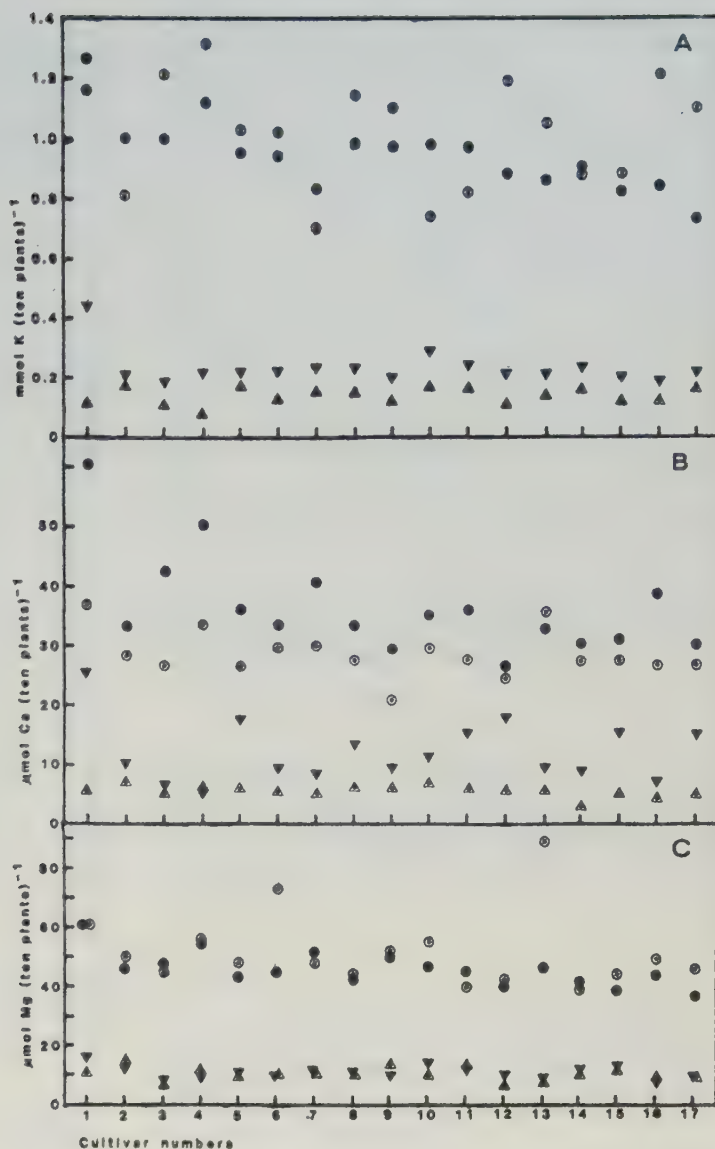
Fig. 3. Contents of nitrogen (A) and accumulation of phosphorus (B) and sulfur (C) in seven-day-old barley seedlings of 17 cultivars. Symbols and cultivar numbers as for Fig. 2. Values are means of three replicates. SE usually less than 9% (nitrogen) or 6% (phosphorus and sulfur).

contents were about constant all through cultivation in N-free nutrient solution (Tab. 3), which indicates that efflux of nitrogenous compounds was small. The proportions of N retained in the roots was about 20% (Tab. 4) for all cultivars ('Salve' 20%, 'Mona' 21%, 'Kajsa' 16% and 'Ingrid' 22%), and did not change during cultivation in N-free nutrient solution. There were no significant differences among the cultivars in use-efficiency of N either before or after the switch from N-containing to N-free nutrient solution (Tab. 3).

Discussion

Seeds of cultivars of barley differ in dry weight and mineral content (Tab. 1 and Rasmusson et al. 1972, Metivier and Dale 1977a). Variation of N contents of seeds may also result from differences in the prior cultivation conditions of the parent (Metivier and Dale 1977a). These differences contribute to variation in mineral nutrition of young barley plants. The importance of endogenous minerals decreases with the age of the seedlings, if exogenous nutrient supply is sufficient. Varietal differences in N content in seeds will lose their importance if the element is supplied at a non-growth-

Fig. 4. Contents of potassium (A), calcium (B) and magnesium (C) in seven-day-old barley seedlings of 17 cultivars. Symbols and cultivar numbers as for Fig. 2. Values are means of three replicates. SE usually less than 12%.



limiting level soon after germination (Metivier and Dale 1977b).

In seven-day-old high-salt seedlings of barley there is still a minor influence of seed properties on varietal differences in mineral nutrition. Total dry weights and total N content of the barley seedlings were correlated (Snedecor and Cochran 1974) to seed content of N (r

Fig. 5. Dry weights for cultivars Salvo, Kajsa, Mona and Ingrid during cultivation in nitrogen-free nutrient solution. Plants were cultivated in nutrient solution with 4.0 mM nitrate for six days, and thereafter in solution without nitrogen. Circles indicate shoots, and triangles, roots. Values are means of three replicates with ten plants each. SE usually less than 9%.



Tab. 2. Relationship between dry weight and contents or accumulation of macro-nutrients in seven-day-old seedlings of 17 cultivars of barley. Plants grown in nutrient solutions with high (A) and low (B) ionic strength. Experimental conditions are described in Fig. 1 (experiments A and B). k and l are constants in the equation: dry weight (g) = k (g/mmol) $\times$ content of mineral element (mmol) + l (g). r is the correlation coefficient. The level of significance of r is indicated by stars: * $0.01 < P < 0.05$ and ** $P < 0.01$.

Element	Experiment	Plant part	k	l	r
N	A	Shoots	0.21	0.020	0.94**
		Roots	0.27	0.006	0.90**
	B	Shoots	0.28	-0.019	0.76**
		Roots	0.44	-0.017	0.95**
P	A	Shoots	0.8	0.36	0.50*
		Roots	0.3	0.136	0.24
	B	Shoots	0.8	0.30	0.34
		Roots	1.5	0.098	0.45
S	A	Shoots	2.2	0.37	0.40
		Roots	1.1	0.138	0.22
	B	Shoots	2.0	0.34	0.19
		Roots	1.2	0.142	0.10
K	A	Shoots	0.40	0.099	0.91**
		Roots	0.124	0.125	0.37
	B	Shoots	0.113	0.26	0.56**
		Roots	0.029	0.145	0.04
Ca	A	Shoots	4	0.34	0.64**
		Roots	0.4	0.148	0.11
	B	Shoots	8	0.130	0.76**
		Roots	9	0.099	0.29
Mg	A	Shoots	7	0.166	0.78**
		Roots	6	0.089	0.68**
	B	Shoots	1.4	0.30	0.47
		Roots	4	0.105	0.42

Tab. 3. Contents and use-efficiency ratios for nitrogen in plants of cultivars Salve, Mona, Kajsa and Ingrid during cultivation in nitrogen-free medium. SE was usually less than 3% (nitrogen content) and 6% (use-efficiency), respectively. Otherwise as for Fig. 5.

Cultivar	Total nitrogen content (mmol) Day				Use-efficiency ratio (g/mmol) Day	
	6	9	12	15	6	15
Salve	1.70	1.45	2.00	1.53	20	43
Mona	1.80	1.94	1.82	1.70	19	46
Kajsa	1.48	1.58	1.50	1.70	19	45
Ingrid	1.46	1.14	1.47	1.34	21	43

values for the high-salt plants were 0.49 for dry weight and 0.52 for N content ($0.01 < P < 0.05$ in both cases); and for low-salt plants the values were 0.45 and 0.36, respectively (both $P > 0.05$). Increase in dry weight between seeds and seven-day-old seedlings can be described by a form of the equation used in Tab. 4A and B: dry weight of seven-day-old seedlings = $(1 + \text{RGR}/100)^7 \times$ dry weight of seeds. When dry weight of

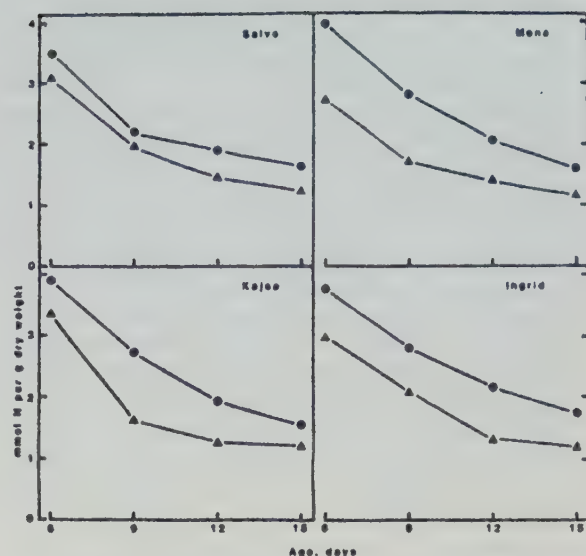


Fig. 6. Nitrogen concentrations in cultivars Salve, Kajsa, Mona and Ingrid during cultivation in nitrogen-free nutrient solution. SE usually less than 5%. Otherwise as for Fig. 5.

seeds and plants were correlated, r values were 0.56 ($0.01 < P < 0.05$) for high-salt plants and 0.26 ($P > 0.05$) for low-salt plants. The r values lower than 1 are due to the variation in RGR between cultivars (see Tab. 4A and B).

Tab. 4A. Average daily increase in dry matter (%) in 17 cultivars of barley. Relative growth rate calculated as: $(1 + \text{RGR}/100)^7 = \text{dry weight of plant}/\text{dry weight of seeds}$. Approximations: 1) Dry weight of seeds at planting = initial dry weight of seeds. 2) Dry weight of remnants of seeds day seven $\ll$ initial dry weight of seeds.

Conditions	Mean $\pm$ SD	Range	
		Upper value	Lower value
High-salt	6.1 $\pm$ 1.9%	9.9%	2.7%
Low-salt	3.3 $\pm$ 2.3%	9.0%	0.0%

4B. Daily increase (%) in dry matter in some cultivars of barley. Calculated from the formula in Tab. 4A.

Cultivar	High-salt plants	Low-salt plants
Salve (1)	7.0	4.6
Kajsa (3)	9.9	5.8
Tellus (11)	4.5	0.0
Edda II (16)	8.4	9.0
Ingrid (17)	5.0	5.6

Figure 2A shows intervarietal differences in root growth for seven-day-old seedlings of barley. Root size and culture method were in most combinations not correlated with the ability to deplete the nutrient solution of N or other elements. Only cultivars with small roots in the high-salt medium, e.g. 'Eva' (cv. 9), 'Tellus' (cv. 11), 'Sv 78 460' (cv. 15) and 'Edda II' (cv. 16) accumulated elements poorly (Figs 2–4). In addition to root size, differences among cultivars of barley in net ion uptake may also be due to different flux rates into and out of the roots (Schimansky and Marschner 1971, Pettersson 1978, Glass and Perley 1980, Jensen and Pettersson 1980, Glass et al. 1981).

The coefficient r in Tab. 2 is an expression of the variability in use-efficiency for specific elements. Use-efficiencies of N in high- and low-salt seedlings, of K and Ca in shoots and of Mg in high-salt seedlings are fairly constant. The low-salt seedlings of 'Salve' had an apparently high use-efficiency of N and other elements (data not shown). This is probably due to the fact that 'Salve' (cv. 1) is the only cultivar that almost, but not completely, depleted the nutrient solution of N (data not shown). Low-salt seedlings of 'Salve' might have been slightly more "N-deficient" than low-salt seedlings of other cultivars, which did not accumulate more than 90% of the supplied N. The lack of variability among different cultivars of barley in use-efficiency of N was also found for older plants (Fig. 6). Insignificant differences in use-efficiency of N were observed in the period between day 6 and day 15 for plants cultivated in N-free nutrient solution (Tab. 3). Varietal differences in use-efficiency of P, S, Mg (only in low-salt plants) and of K and Ca in roots are greater (Tab. 2). However, variations in use-efficiency of K and Ca in roots are of little importance since the bulk of these elements were found in the shoots. Behind genetic variation in use-efficiency lie differences in biochemical and biophysical processes (Whiteaker et al. 1976, Epstein 1978, Chapin and Bielecki 1982).

Transport processes of N compounds in barley seedlings have been discussed by Metivier and Dale (1977a, b) and Dale and Felipe (1978). Our analysis of transport of elements is limited to calculations of percentage of total contents found in roots (Tab. 5). It is

Tab. 5. Mineral elements in roots as % of total plant content or accumulation in seven-day-old barley plants. Values are means of data from 17 cultivars (three replicates each) $\pm$ SE.

Element	High-salt plants	Low-salt plants
Nitrogen	20 $\pm$ 2	21 $\pm$ 2
Phosphorus	26 $\pm$ 4	29 $\pm$ 4
Sulfur	28 $\pm$ 5	23 $\pm$ 3
Potassium	20 $\pm$ 2	12 $\pm$ 4
Calcium	25 $\pm$ 8	16 $\pm$ 2
Magnesium	19 $\pm$ 3	17 $\pm$ 4

evident that varietal differences in partitioning of N between roots and shoots are small.

In conclusion, varietal variation in mineral nutrition among seven-day-old high-salt seedlings of barley, but not among low-salt seedlings, is partly due to variation in seed contents of elements (Tab. 1). Relative growth rate varies greatly among seedlings of cultivars of barley and between high- and low-salt seedlings, and this might create differences in demand for nutrients (Tab. 4A and B and Chapin and Bielecki 1982). There are also varietal differences in properties such as root size and uptake, use-efficiency and root/shoot-partitioning of mineral elements (Epstein 1972). For P, S and Mg (low-salt conditions) all these factors were important, but for K and Ca differences in use-efficiency between cultivars were smaller (Figs 2A, 3B–C and 4A–C, Tabs 2 and 5). Variation in use-efficiency of Ca in shoots and of Mg during high-salt conditions was small (Tab. 2). Varietal differences in N economy of barley seedlings are mainly affected by differences in root size and uptake of the elements (Figs 2A and 3A). The contribution of differences in use-efficiency and root/shoot-partitioning of N are comparatively small.

Acknowledgements – The authors thank Mrs Lena Lundh for skilful technical assistance and Dr Mike Coverley, Mrs Mary Neighbours and Dr Tom Vogelmann for correction of the language. Seeds were kindly provided by Svalöf AB, Svalöv, Sweden. The work was supported by grants from the Swedish Council for Forestry and Agricultural Research.

References

- Chapin, F. S. & Bielecki, R. L. 1982. Mild phosphorus stress in barley and a related low-phosphorus-adapted barley-grass: Phosphorus fractions and phosphate absorption in relation to growth. – *Physiol. Plant.* 54: 309–317.
- Clark, R. B. 1982. Plant genotype differences to uptake, translocation, accumulation and use of mineral elements. – *In* Genetic Specificity of Mineral Nutrition of Plants (M. R. Saric, ed.), pp. 41–55. The Serbian Academy of Sciences and Arts, Belgrade.
- & Brown, J. C. 1980. Role of the plant in mineral nutrition as related to breeding and genetics. – *In* Moving up the Yield Curve: Advances and Obstacles (L. S. Murphy, E. Doll and L. F. Welch, eds), pp. 45–70. American Society of Agronomy, Madison, WI. ISBN 0-89118-064-8.
- Clarkson, D. T. & Hanson, J. B. 1980. The mineral nutrition of higher plants. – *Annu. Rev. Plant Physiol.* 31: 239–298.
- Dale, J. E. & Felipe, G. M. 1977. Nitrogen movement into and out of the first leaf of barley. – *Z. Pflanzenphysiol.* 84: 77–83.
- Doddema, H. & Telkamp, G. P. 1979. Uptake of nitrate by mutants of *Arabidopsis thaliana*, disturbed in uptake or reduction of nitrate. II. Kinetics. – *Physiol. Plant.* 45: 332–338.
- Epstein, E. 1972. Mineral Nutrition of Plants: Principles and Perspectives. – John Wiley and Sons, New York. pp. 325–344. ISBN 0-471-24330-X.
- 1978. An inborn error of potassium metabolism in the tomato *Lycopersicon esculentum*. – *Plant Physiol.* 62: 582–585.

- & Jefferies, R. L. 1964. The genetic basis of selective ion transport in plants. - *Annu. Rev. Plant Physiol.* 15: 169-184.
- Gabelman, W. H. 1976. Genetic potentials in nitrogen, phosphorus and potassium efficiency. - *In Proceedings of Workshop on Plant Adaption to Mineral Stress in Problem Soils* (M. J. Wright, ed.), pp. 205-212. National Agricultural Library, Beltsville, MD.
- & Gerloff, G. C. 1982. The search for, and interpretation of, genetic controls that enhance plant growth under deficiency levels of a macronutrient. - *In Genetic Specificity of Mineral Nutrition of Plants* (M. R. Saric, ed.), pp. 301-312. The Serbian Academy of Sciences and Arts, Belgrade.
- Gerloff, G. C. 1963. Comparative mineral nutrition of plants. - *Annu. Rev. Plant Physiol.* 14: 107-124.
- 1976. Plant efficiencies in the use of nitrogen, phosphorus and potassium. - *In Proceedings of Workshop on Plant Adaption to Mineral Stress in Problem Soils* (M. J. Wright, ed.), pp. 161-173. National Agricultural Library, Beltsville, MD.
- Glass, A. D. M. & Perley, J. E. 1980. Varietal differences in potassium uptake by barley. - *Plant Physiol.* 65: 160-164.
- , Siddiqui, M. Y. & Giles, K. I. 1981. Correlations between potassium uptake and hydrogen efflux in barley varieties. A potential screening method for the isolation of nutrient efficient lines. - *Plant Physiol.* 68: 457-459.
- Hackett, C. 1968. A study of the root system of barley. I. Effects of nutrition on two varieties. - *New Phytol.* 67: 287-300.
- Jensén, P. & Pettersson, S. 1980. Varietal variation in uptake and utilization of potassium (rubidium) in high-salt seedlings of barley. - *Physiol. Plant.* 46: 411-415.
- Lindemann, W. 1958. Observation on the behaviour of phosphate compounds in *Chlorella* at the transition from dark to light. - *In Proceedings of the 2nd International Conference on the Peaceful Uses of Atomic Energy* Vol. 24 pp. 8-15.
- Läuchli, A. 1976. Genotypic variation in transport. - *In Encyclopedia of Plant Physiology. New Series* (U. Lüttge and M. G. Pitman, eds), Vol. IIB, pp. 372-393. Springer-Verlag, Berlin. ISBN 3-540-07453-8.
- Metivier, J. R. & Dale, J. E. 1977a. The utilization of endosperm reserves during early growth of barley cultivars and the effect of time of application of nitrogen. - *Ann. Bot.* 41: 715-728.
- & Dale, J. E. 1977b. The effects of grain nitrogen and applied nitrate on growth, photosynthesis and protein content of the first leaf of barley cultivars. - *Ann. Bot.* 41: 1287-1296.
- Pettersson, S. 1978. Varietal differences in rubidium uptake efficiency of barley roots. - *Physiol. Plant.* 44: 1-6.
- Rasmuson, D. C., Hester, A. J., Fick, G. N. & Byrne, I. 1971. Breeding for mineral content in wheat and barley. - *Crop Sci.* 20: 623-626.
- Saric, M. R. (ed.). 1982. Genetic Specificity of Mineral Nutrition of Plants. The Serbian Academy of Sciences and Arts. Belgrade. 386 p.
- Schimansky, C. & Marschner, H. 1971. Suitability of ^{86}Rb as a tracer for potassium in studies relating to potassium uptake by maize, sugarbeet and four varieties of barley. - *Z. Pflanzenernähr.* 129: 141-147.
- Snedecor, G. W. & Cochran, W. G. 1974. Statistical Methods. - The Iowa State University Press, Ames. IA. pp. 172-198, 577. ISBN 0-8138-1560-6.
- Vose, P. B. 1963. Varietal differences in plant nutrition. - *Herb. Abstr.* 33: 1-13.
- Whiteaker, G., Gerloff, G. C., Gabelman, W. H. & Lindgren, D. 1976. Intraspecific differences in growth of beans at stress levels of phosphorus. - *J. Am. Soc. Hortic. Sci.* 101: 472-475.
- Wright, M. J. (ed.). 1976. Proceedings of Workshop on Plant Adaption to Mineral Stress in Problem Soils. - National Agricultural Library, Beltsville, MD. 420 p.

Net uptake and partitioning of nitrogen and potassium in cultivars of barley during ageing

Harald Perby and Paul Jensén

Perby, H. and Jensén, P. 1984. Net uptake and partitioning of nitrogen and potassium in cultivars of barley during ageing. – *Physiol. Plant.* 61: 559–565.

Experiments were carried out with barley cultivars (*Hordeum vulgare* L.) grown in both pot- and water-culture. Net uptake of NO_3^- and K^+ in the roots was followed in two barley cultivars grown on water-culture for 85 days. After an initial period of low net uptake of both ions, uptake increased until a maximum was reached after 30 to 45 days. Thereafter, net uptake of NO_3^- and K^+ steadily decreased. In the pot experiments, effects of different mineral supply on day 4 to 18 upon the development of five barley cultivars of various earliness were investigated. The effect of earliness on fresh weight production was largest when mineral supply on day 4 to 18 was limited. The influence of limited mineral supply on day 4 to 18 on K-economy was independent of earliness of the cultivars. The maximal N-content was reached at the same time as maximal fresh and dry weight in fairly late cultivars; in early cultivars maximum N-level was reached later than maximum fresh and dry weight. Overall, maximal N-content was higher in the fairly late cultivars than in the early cultivars. The highest rate of ^{15}N -transport was attained later in two of three fairly late cultivars than in early cultivars. Partitioning of dry weight, N and K in the shoots changed during ageing, ears being an important sink. Varietal differences in partitioning depended on the earliness of the cultivars. The largest fraction of recently supplied ^{15}N , supplied as nitrate, and K^+ (^{86}Rb) were found in the stems. In the oldest plants of the early cultivars the transport to the ears of these isotopes was gradually impaired, reflecting the decreasing function of the long distance transport system.

Additional key words – Distribution, early cultivar, late cultivar, ^{15}N , ^{86}Rb , translocation, varietal differences.

H. Perby (reprint requests) and P. Jensén, Dept of Plant Physiology, Univ. of Lund, Box 7007, S-220 07 Lund, Sweden.

Introduction

Much of the information on ion fluxes into and out of roots and translocation and utilization of nutrients in plants emerges from experiments with seedlings of cereals. A problem in the topic of mineral nutrition of plants is, however, that the processes involved change during the life span of the plants. Jensén (1978) studied uptake of K^+ (^{86}Rb) and SO_4^{2-} by wheat plants grown on water culture during 104 days. He found that not only the amounts of ions absorbed per specimen and unit of time but also the relative importance of active and passive uptake and root-shoot-partitioning of the elements

changed when the plants became older. Thus, conclusions drawn from experiments with young plants may not be valid for older plants and investigations starting at anthesis will miss important preanthesis events.

Many authors have compiled information about varietal differences in mineral nutrition (some important contributions are listed by Perby and Jensén 1983), but only a few physiological studies in this field deal with older plants. Lundegårdh (1932, 1951) summarized some early studies of varietal differences in mineral economy in oat and wheat. Distribution of K, Mg, Ca and P varied in a manner specific for both the element and the cultivar. Waldren and Flowerday (1979) de-

Received 9 December, 1983; revised 18 April, 1984

scribed ten stages of growth in winter wheat and correlated changes in distribution of N, P and K to changes in morphology during ageing. Lambers et al. (1982) and Simpson et al. (1982, 1983) introduced a model for nitrogen transport in vegetative and generative wheat plants. Shoots of vegetative plants were found to exert control over the nitrogen content in the roots, partly by extensive recycling of the element. In grain-filling plants a considerable fraction of the N from the leaves first passed the roots on the way to the grains. Crawford et al. (1982) were able to model uptake and redistribution of N in maize, classifying parts of the plants as primary or secondary sources and sinks for N. The uptake of N and the distribution of various N-compounds differ significantly between inbreds and hybrids of maize during ageing (Chevalier and Schrader 1977).

The aim of the present investigation was to follow uptake of NO_3^- and K^+ during the lifespan of some cultivars of barley and to study partitioning of N and K after emergence of ears. The results obtained are related to the earliness of the cultivars. Varietal differences in uptake and utilization of six macro-elements in seedlings of the cultivars included in the present experiments were studied by Perby and Jensén (1983).

Materials and methods

Cultivars of barley (*Hordeum vulgare* L.) used in the experiments are listed in Tab. 1.

Water culture experiment

Seeds of 'Bonus' and 'Hellas' were soaked and germinated in darkness on moist filter paper in petri dishes at

22°C. After three days, the seedlings were inserted through holes drilled through round plastic discs, 35 mm in diameter. Four groups of each cultivar, with ten seedlings in each group, were placed in 2 l black-painted glass beakers (one group per beaker) with 1800 g aerated nutrient solution. The solution contained 1.0 mM $\text{Ca}(\text{NO}_3)_2$, 1.0 mM KNO_3 , 1.0 mM MgSO_4 , 1.0 mM KH_2PO_4 , 0.5 mM K_2HPO_4 , 0.1 mM Fe-EDTA, and micro-nutrients (except Fe) as given by Hewitt and Smith (1975). The pH was about 6.1. The culture solution was, with few exceptions, changed before the levels of NO_3^- and K^+ were reduced below 1.0 mM. Water losses from the beakers were replaced every second day with distilled water. Similarly grown plant groups were harvested on day 8 and 33 for determination of fresh weight.

Plants were grown in a climate chamber at a temperature of $25 \pm 1^\circ\text{C}$, a relative humidity of about 50% and under continuous light (irradiance about 25 W m^{-2} , General Electric F48 Power Groove 17 CVX fluorescent lamps).

Each beaker was weighed after the uptake experiment. After stirring, 50 ml solution from each beaker was transferred to a plastic beaker with 3 ml of a solution with approximately 2.5 M Na_2SO_4 and 0.33 M H_3BO_3 . The sealed samples were stored cold and dark.

Samples equilibrated to 25°C were analyzed with Orion electrodes 93-19 for K^+ and 93-07 for NO_3^- , both electrodes connected to an Orion model 701A ion analyzer with an interface for simultaneous use of two electrodes. K determinations were calibrated with KNO_3 solutions in the range from 1.0 to 3.5 mM and NO_3^- determinations by a known addition to the same solutions.

Pot experiments

Seeds of barley (30 in experiment A and 25 in experiment B in each pot) were sown in plastic pots with 3 l silversand No 95. The pots were placed on large plastic discs in a greenhouse and watered with 0.35 l distilled water. After seven days, the seedlings in each pot were reduced to 20 healthy specimens. The design of the pot experiments is summarized in Fig. 1.

Sunlight in the greenhouse was supplemented with mercury lamps (Philips 400 W, total irradiance $80\text{--}90 \text{ W m}^{-2}$). The daylength was 18 h. Temperature was $20 \pm 1^\circ\text{C}$ and relative humidity ca 65%. Uptake experiments (Fig. 1) were conducted in climate chambers with conditions as for the water culture experiment.

At harvest, the shoots were divided into stems, senescent leaves, leaves and ears. In experiment A (Fig. 1) all plant parts were dried at 70°C for three days. A part of each sample was digested in a 2:1 mixture of HNO_3 and HClO_4 . The content of K^+ (Fig. 1) was then determined by atomic absorption spectrophotometry. ^{86}Rb was measured by liquid scintillation spectrometry. Total content of nitrogen was determined titrimetrically by an

Tab. 1. Spring barley cultivars used in the experiments. Cultivars classified according to earliness by G. Persson, Svalöf AB (personal communication). Numbers of cultivars refer to ranking in Perby and Jensén (1983).

Cultivar	Main cultivation area	Comment
Very early Kajsa (3)	Northern Sweden	—
Early Mona (8)	South Sweden	Disappearing from the market
Fairly late Salve (1)	Middle Sweden	Disappeared from the market
Bonus (5) Nürnberg II (7)	South Sweden Germany	— Variety from about 1833
Alva (10) Hellas (12)	South Sweden South Sweden	— Disappeared from the market
Ingrid (17)	South and middle Sweden	—

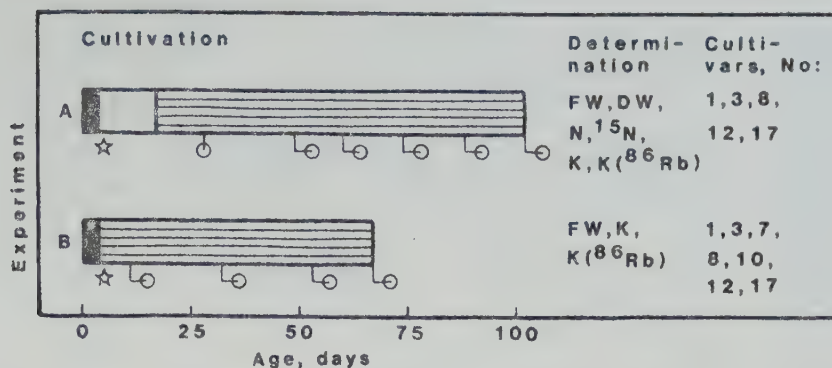


Fig. 1. Design of pot experiments. Cultivars are indicated by numbers (see Tab. 1). Pots were protected from light until day 4 (black area). On day 5 mercury lamps were turned on (stars). Nutrient solutions were supplied at the rate of removal (0.25 to 0.50 l per pot) every second day, starting from day 4. The dishes on which the pots were placed were washed every tenth day. Lined area indicates cultivation with full strength medium: 2.0 mM KNO₃, 1.0 mM Ca(NO₃)₂, 1.0 mM MgSO₄, 1.0 mM KH₂PO₄, 0.5 mM Na₂HPO₄, 0.2 mM Fe-EDTA, 0.5 μM MnSO₄ and 1.5 μM H₃BO₃, pH 6.1. White area indicates cultivation in half strength medium. Vertical bars below lined

areas indicate transfer of pots to a climate chamber, where uptake experiments started 24 h later. At the start of an uptake experiment each pot was watered from the top with 0.5 l labelled medium (full strength medium containing ⁸⁶Rb⁺ and in experiment A from day 61 also NO₃ with 96 atomic % ¹⁵N). In addition, 0.25 l of the same medium was added to each dish. Labelled medium, 0.25 and 0.5 l, respectively, was added to each dish 24 and 48 h later. Harvest of four parallel samples of each cultivar three days after the first supply of labelled medium is indicated by rings. In experiment A, no uptake experiment was done on day 28 before harvest.

automatic Kjeldahl technique (Tecator Kjeltac 1003) modified for efficient reduction of NO₃⁻. Percentages of ¹⁵N were determined by optical ¹⁵N-analysis (Packard NOI-5) of dried, evacuated and vapourized samples of the titrated solution.

Results

Continuous measurement of net uptake of NO₃⁻ and K⁺

Increase in fresh weight and daily net uptake of NO₃⁻ and K⁺ by cultivars Hellas and Bonus over 85 days are shown in Fig. 2. The course of net ion uptake was similar for both cultivars during the entire culture period; uptake increased until a maximum was reached, whereafter a steady decline was observed. The main differences between the cultivars are that maximal net uptake of NO₃⁻ and K⁺ occurred later in Bonus and that net uptake of both ions was higher in Hellas in the 20- to 40-day-old plants. After day 50 the situation was reversed, and uptake was then higher in Bonus.

Effects of early mineral supply on growth and uptake

The mineral supply on day 4 to 18 (Fig. 1, experiments A and B) affected the development of barley plants cultivated in sand. Maximal fresh weight coincided with maximal K⁺-content (Fig. 3) in plants supplied with full strength medium from day 4. For plants supplied with only half-strength medium on day 4 to 18, the maximal K⁺-content of the shoots was reached before or at the same time as maximal fresh and dry weight of the shoots (Fig. 3). Maximal N-content in the shoots of these plants was obtained at the same time as (fairly late cvs

Salve, Hellas and Ingrid) or later than (very early Kajsa and early Mona) maximal fresh and dry weight of the shoots (Fig. 3).

The transport of recently supplied K⁺ (⁸⁶Rb) to the

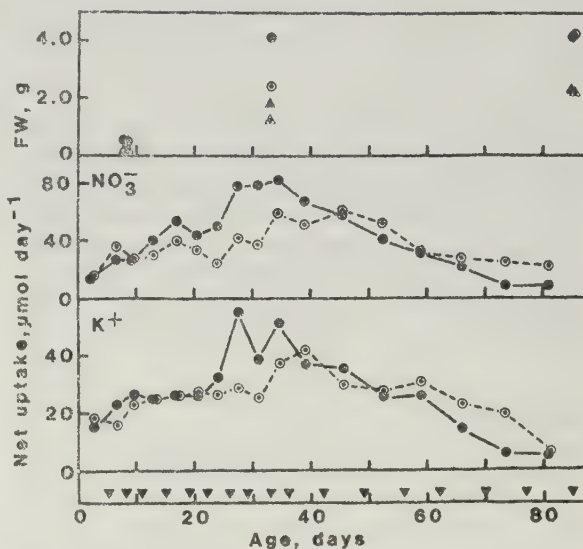


Fig. 2. Fresh weight and net uptake per plant and day of NO₃⁻ and K⁺ by Hellas (filled symbols) and Bonus (open symbols) during 85 days in water culture. Changes of nutrient solution are indicated by water triangles at the bottom of the figure. Fresh weights of shoots (circles) and roots (triangles) are plotted on the day of harvest. Mean values for net uptake per plant and day are plotted midway between the sampling days and connected by lines. Coinciding points are separated horizontally. Values are means of four replicates. SE were usually less than 15 (before day 33) and 30 (after day 33) % of means.

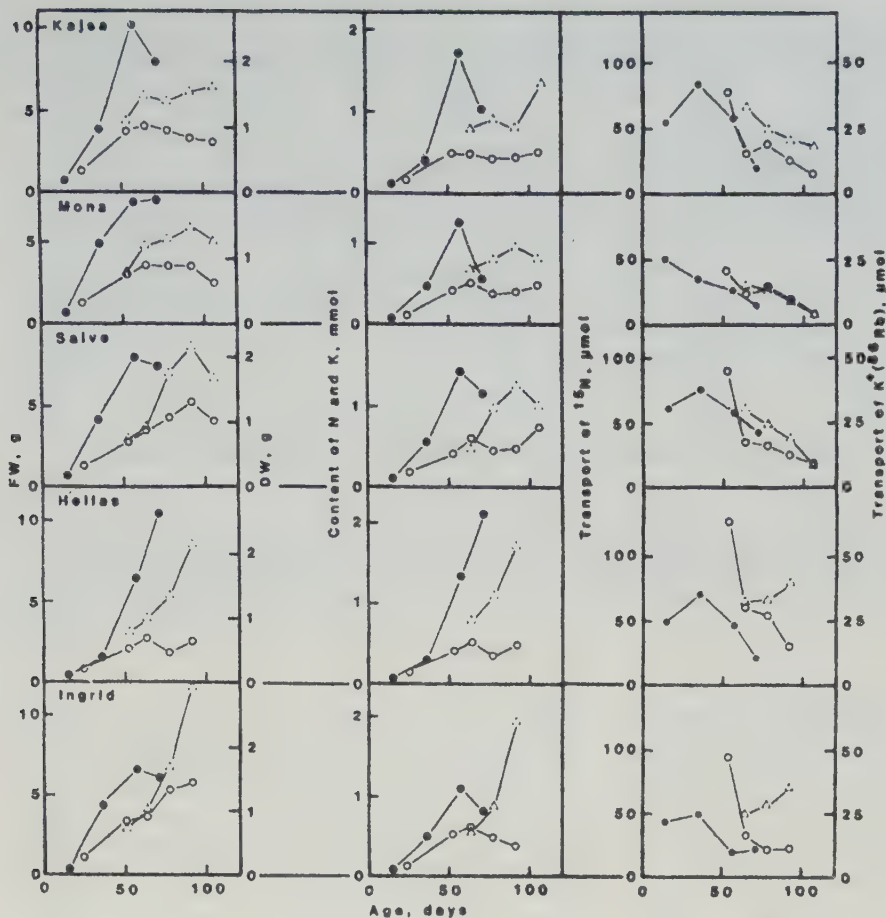


Fig. 3. Fresh weight and dry weight (left), contents of N and K (middle) and transport during 72 h of ^{15}N and K^+ (^{86}Rb) (right) per shoot of five cultivars of barley. Filled circles indicate fresh weight, K^+ -content and K^+ (^{86}Rb)-transport for plants supplied full strength medium from day 4. Unfilled circles indicate the same parameters for plants given half-strength medium day 4 to 18. Triangles indicate dry weight. N-content and ^{15}N -transport for plants supplied half-strength medium day 4 to 18. Values are means of four replicates. SE were usually less than 10 (fresh weight), 15 (dry weight) or 20% (contents and transport of N and K) of means.

shoots decreased independently of nutritional regime on day 4 to 18 as the plants became older (Fig. 3). In contrast, a very late maximal transport of ^{15}N was recorded in two of three fairly late cultivars, Hellas and Ingrid, but not in Salve or in the early cultivars Kajsa and Mona. In the case of Hellas this contrasts to the results obtained from the experiment with the water culture grown plants (Fig. 2). Cultivars Alva and Nürnberg II are not shown in Fig. 3 since they were only included in experiment B (Fig. 1) and behaved as the other fairly late cultivars.

Partitioning of N and K in the shoots

Partitioning of dry matter between different parts of the shoots changed with increasing age of the plants (Fig. 4). On day 53 most of the dry matter was found in the stems, but in the early cultivars the ears also contained a considerable fraction. In the early late cultivars dry matter in the ears constituted an ever increasing part of the total shoot dry weight, while no clear trend was found for the early cultivars.

Compared with partitioning of dry matter, partition-

ing of N between various shoot parts was different between day 64 and 106, although the trend was the same as for dry matter for both types of cultivars (Fig. 4). In contrast to dry matter allocation, ears and leaves of all cultivars contained relatively more N than the stems. A negligible fraction of N was found in senescent leaves. Losses of N through shedding of leaves can therefore not seriously affect the N economy of these barley cultivars.

Similar to distribution of dry weight, retranslocation to the ears of a relatively large part of the total shoot-N occurred earlier in Kajsa and Mona than in the other cultivars. Partitioning in the shoots of recently absorbed ^{15}N and the changes in partitioning of this N-fraction as the plants aged, contrasted to the distribution of N in the shoots (Fig. 4). As compared with total N distribution relatively more of the recently absorbed ^{15}N was found in the stems of both early and fairly late cultivars. In the fairly late cultivars the pattern of distribution of ^{15}N was more or less the same during the whole experiment, but in the early cultivars the transport of ^{15}N to the ears decreased.

Most of the total K^+ -content in the shoots was generally found in the stems, but as the plants aged a consid-

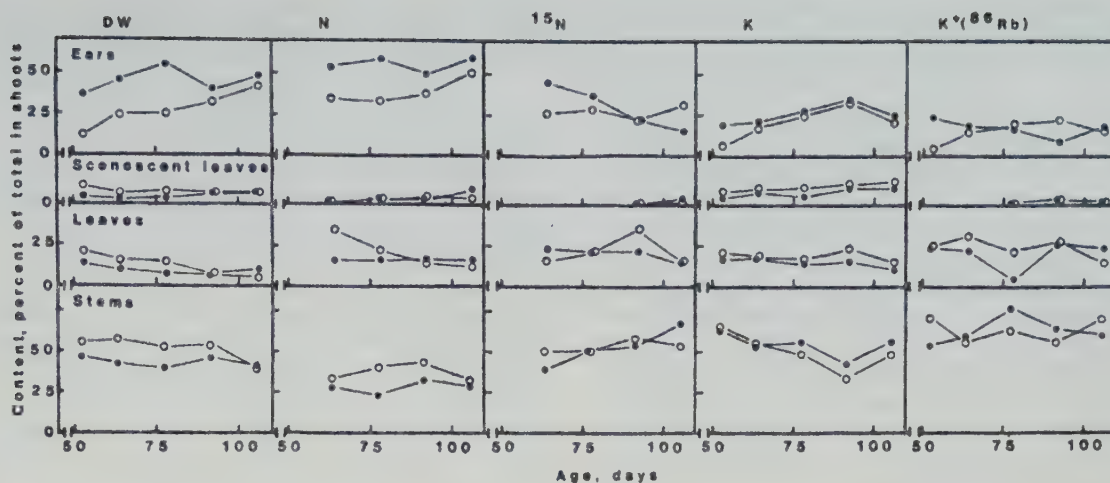


Fig. 4. Partitioning of dry weight, N, ^{15}N , K and K^+ (^{86}Rb) as percentages of total in old shoots of early (Kajsa and Mona) and fairly late (Salve, Hellas and Ingrid) cultivars of barley. The plants were supplied half-strength medium days 4 to 18. ^{15}N and ^{86}Rb were supplied during the last 72 h before harvest. Filled symbols indicate means for the early cultivars and unfilled symbols indicate means for the fairly late cultivars. SD never exceeded 4 (dry weight), 8 (N-content), 20 (^{15}N -transport), 13 (K-content) and 23% [K^+ (^{86}Rb)-transport].

erable fraction was translocated to the ears (Fig. 4). In the same way as for dry weight and total nitrogen content, K^+ -retranslocation to the ears began early in Kajsa and Mona. Changes in distribution of recently absorbed K^+ (^{86}Rb) during ageing depended on the earliness of the cultivars. In both early and fairly late cultivars most of the K^+ (^{86}Rb) was found in the stems. At the end of the experiment the percentage of K^+ (^{86}Rb) translocated to the ears of fairly late cultivars increased, while it decreased in early cultivars.

Discussion

The net uptake of NO_3^- and K^+ per specimen by two cultivars of barley follows a similar course as the plant's age (Fig. 2). Three stages are distinguishable (but not clearly separable) for the plants grown in water culture: 1) A low net ion uptake by seedlings; 2) an increasing net uptake during a period with rapid vegetative development; 3) a steady decline in net ion uptake in older stages. A similar development in winter wheat has been described by Erdei et al. (1983). In wheat most N is accumulated after the leaf sheaths begin to elongate and before heading (Waldren and Flowerday 1979). Differences between Hellas and Bonus are found in the timing of the three stages of net uptake of NO_3^- and K^+ and in net uptake of the elements during specific periods (Fig. 2). Similar changes in mineral uptake may be found among field-grown plants, although mineral accumulation under field conditions is strongly influenced by the environment (Gregory et al. 1981).

Rankings of cultivars of barley according to their ability to absorb K^+ have been made for seedlings by Pettersson (1978), Glass and Perley (1980), Jensén and

Pettersson (1980) and Glass et al. (1981). Influx and sometimes efflux of K^+ ($\text{g fresh weight}^{-1}$) of roots during relatively short periods have been determined by different methods. There are, based on the following observations, objections against a direct practical application of such results: 1) Uptake of K^+ (^{86}Rb) ($\text{g fresh weight}^{-1}$) of root changes with age in wheat (Jensén 1978); 2) root growth proceeds differently among cultivars of barley (Hackett 1968); 3) net uptake of NO_3^- and K^+ develops specifically for each cultivar (Fig. 2). To be of practical use, studies of varietal differences in mineral uptake must be expanded over a substantial period of time, as has been done by Siddiqi and Glass (1982).

Growth of barley is a sequence of events (Briggs 1978). The seedlings are established during a period of low growth rate. The plants then enter the 'grand period of growth'. Although contents and net uptake rates of minerals in seedlings are low compared with those of older plants, the supply of N to seedlings of barley has proved to be of great importance. Marriott and Dale (1977) and Metivier and Dale (1977) have shown that, when application of NO_3^- to seedlings is delayed beyond day 4, it results in lower dry weight, N-content and CO_2 -fixation on day 14. Some effects shown in Fig. 3 may be explained by the differential N-supply on day 4 to 18. The variation in K-supply is possibly of less importance, since attainment of maximal K-content precedes attainment of maximal fresh weight in some plants supplied with half-strength medium on day 4 to 18.

The length of the 'grand period of growth' varies for the cultivars and depends on the nutrient supply on day 4 to 18 (Fig. 3). Transport to the shoots of recently absorbed ^{15}N and K^+ (^{86}Rb) changes in a pattern specific

for each cultivar and declines before maximal fresh weight is reached. This indicates that stage 2 in the uptake of NO_3^- and K^+ does not equal the 'grand period of growth' for the plants grown in pots (Fig. 3).

Plants grown with full strength medium from day 4 reach maximal fresh weight at approximately the same time, independent of type of cultivar. In contrast, plants supplied half-strength medium on day 4 to 18, show differences in attainment of maximal fresh weight, which is in accordance with the earliness of the cultivars (Fig. 3, Tab. 1).

Independent of the earliness of the cultivars, the highest K^+ -content in the shoots is reached at almost the same time for all cultivars (Fig. 3). Maximal N-content occurs late and at approximately the same time in all cultivars, but is generally higher in fairly late cultivars. Similarly, the time-dependent development of uptake of ^{15}N and K^+ (^{86}Rb) by the shoots is not related to the earliness of the cultivars, except in Hellas and Ingrid. Maximal incorporation of ^{15}N is late in these fairly late cultivars (Fig. 3). Correspondingly, wheat might absorb a considerable fraction of the total N-content after anthesis (Spiertz and Ellen 1978, Gregory et al. 1981).

The intervarietal differences in partitioning of dry matter, N and K are related to the earliness of the cultivars (Fig. 4). At the beginning of the partitioning studies, very early Kajsa and early Mona have proportionally larger ears than the three fairly late cultivars. This difference is also observed for partitioning of N and K in the shoots (Fig. 4). Differences in earliness do not seem to create varietal differences in partitioning of recently absorbed ^{15}N or K^+ (^{86}Rb) (Fig. 4).

Partitioning of ^{15}N and K^+ (^{86}Rb) in the shoots of the five cultivars of barley after anthesis (Fig. 4) reflects the influence of ageing on transport of recently absorbed N and K. In cereals, N is supposed to reach the ears mainly in reduced forms via the phloem (Simpson et al. 1983). Most grain-N is retranslocated from other plant parts, but a considerable fraction may be absorbed from the external medium after anthesis (Gregory et al. 1981). In contrast to N and P, only a small, slowly increasing share of the shoot-K is found in the grains of wheat during grain-filling (Spiertz and Ellen 1978). The small amounts of K in the grains can be supposed to be mainly retranslocated by the phloem from other plant parts, since the direct contact between the xylem vessels of the rachilla and the pericarp in wheat and other grasses is prevented by a barrier (Zee and O'Brien 1970). Zee and O'Brien (1971) have also shown the existence of transfer cells in spikelets of wheat, but it is questionable if they move K from the xylem to the phloem. No K^+ (^{86}Rb) was found in grains of grain-filling winter wheat after a 5 h uptake period, although the element was present in other parts of the ears (Erdei et al. 1983, A. Bérczi, personal communication). This evidence indicates that K^+ is transported to the ears by both the xylem and phloem, whereas the grains receive K primarily from the phloem. The relatively

long K^+ (^{86}Rb)-exposure in our experiment make possible both a xylem-mediated transport of this element to the non-grain parts of the ears and a substantial phloem-mediated retranslocation to the grains.

Figure 4 shows that stems and leaves incorporate a large fraction of recently absorbed ^{15}N and K^+ (^{86}Rb). This is in accordance with the hypothesis that parenchyma cells have an important role in reduction of NO_3^- and in xylem-to-phloem transfer of N (Crawford et al. 1982, Lambers et al. 1982, Simpson et al. 1982, 1983). In leaves of grain-filling cereals, K^+ is supposed to stimulate phloem transport (Beringer and Haeder 1981, Mengel et al. 1981). In our experiment ageing of the long-distance transport system proceeds differently in early and fairly late cultivars. The fairly late cultivars show no real sign of ceasing function of long-distance transport of ^{15}N and K^+ (^{86}Rb), except for a decreasing transport of K^+ (^{86}Rb). In the early cultivars changes in transport and partitioning of ^{15}N and K^+ (^{86}Rb) indicate a cessation in function of the long-distance transport system (Figs 3 and 4).

Acknowledgements – We thank Mrs Lena Lundh, Mr Ingvar Jönsson and Mr Birger Nilsson for skilful technical assistance and Ms Mary Neighbours and Dr Tom Vogelmann for correction of the language. Seeds were kindly provided by Svalöf AB, Svalöv, Sweden. The work was supported by grants from the Swedish Council for Forestry and Agricultural Research and P. O. Lundells Foundation.

References

- Beringer, H. & Haeder, H. E. 1981. Influence of potassium nutrition on starch synthesis in barley grains. – *Z. Pflanzenernähr. Bodenk.* 144: 1–7.
- Briggs, D. E. 1978. Barley. – Chapman and Hall Ltd, London. pp. 222–291. ISBN 0-412-11870-X.
- Chevalier, P. & Schrader, L. E. 1977. Genotypic differences in nitrate absorption and partitioning of N among plant parts in maize. – *Crop Sci.* 17: 897–901.
- Crawford, T. W., Rendig, V. V. & Broadbent, F. E. 1982. Sources, fluxes and sinks of nitrogen during early reproductive growth of maize (*Zea mays* L.). – *Plant Physiol.* 70: 1654–1660.
- Erdei, L., Oláh, Z. & Bérczi, A. 1983. Nutrition of winter wheat during the life cycle. II. Influx and translocation of potassium and phosphorus. – *Physiol. Plant.* 58: 131–135.
- Glass, A. D. M. & Perley, J. E. 1980. Varietal differences in potassium uptake by barley. – *Plant Physiol.* 65: 160–164.
- , Siddiqi, M. Y. & Giles, K. I. 1981. Correlations between potassium uptake and hydrogen efflux in barley varieties. A potential screening method for the isolation of nutrient efficient lines. – *Plant Physiol.* 68: 457–459.
- Gregory, P. J., Marshall, B. & Biscoe, P. V. 1981. Nutrient relations of winter wheat. 3. Nitrogen uptake, photosynthesis of flag leaves and translocation of nitrogen to grain. – *J. Agric. Sci.* 96: 539–547.
- Hackett, C. 1968. A study of the root system of barley. I. Effects of nutrition on two varieties. – *New Phytol.* 67: 287–300.
- Hewitt, E. J. & Smith, T. A. 1975. Plant Mineral Nutrition. – The English Universities Press Ltd, London. p. 32. ISBN 0-340-05086-1.

- Jensén, P. 1978. Changes in ion transport in spring wheat during ontogenesis. – *Physiol. Plant.* 43: 129–135.
- & Pettersson, S. 1980. Varietal variation in uptake and utilization of potassium (rubidium) in high-salt seedlings of barley. – *Physiol. Plant.* 48: 411–415.
- Lambers, H., Simpson, R. J., Beilharz, V. C. & Dalling, M. J. 1982. Growth and translocation of C and N in wheat (*Triticum aestivum*) grown with a split root system. – *Physiol. Plant.* 56: 421–429.
- Lundegårdh, H. 1932. Die Nährstoffaufnahme der Pflanze. – Verlag von Gustaf Fischer, Jena. pp. 122–198.
- 1951. Leaf Analysis. – Hilger & Watts Ltd, London. pp. 15–22.
- Marriott, C. & Dale, J. E. 1977. Effects of time of application of nitrate and leaf shading on root growth of plants of *Hordeum vulgare* L. grown in sand and in solution culture. – *Z. Pflanzenphysiol.* 81: 377–385.
- Mengel, K., Secer, M. & Koch, K. 1981. Potassium effect on protein formation and amino acid turnover in developing wheat grain. – *Agron. J.* 73: 74–78.
- Metivier, J. R. & Dale, J. E. 1977. The utilization of endosperm reserves during early growth of barley cultivars and the effect of time of application of nitrogen. – *Ann. Bot.* 41: 715–728.
- Perby, H. & Jensén, P. 1983. Varietal differences in uptake and utilization of nitrogen and other macro-elements in seedlings of barley, *Hordeum vulgare*. – *Physiol. Plant.* 58: 223–230.
- Pettersson, S. 1978. Varietal differences in rubidium uptake efficiency of barley roots. – *Physiol. Plant.* 44: 1–6.
- Siddiqi, M. Y. & Glass, A. D. M. 1982. Studies of the growth and mineral nutrition of barley varieties. I. Effect of potassium supply on the uptake of potassium and growth. – *Can. J. Bot.* 61: 671–678.
- Simpson, R. J., Lambers, H. & Dalling, M. J. 1982. Translocation of nitrogen in a vegetative wheat plant (*Triticum aestivum*). – *Physiol. Plant.* 56: 11–17.
- , Lambers, H. & Dalling, M. J. 1983. Nitrogen redistribution during grain growth in wheat (*Triticum aestivum* L.). IV. Development of a quantitative model of the translocation of nitrogen to the grain. – *Plant Physiol.* 71: 7–14.
- Spiertz, J. H. J. & Ellen, J. 1978. Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilization of assimilates and nutrients. – *Neth. J. Agric. Sci.* 26: 210–231.
- Waldren, R. P. & Flowerday, A. D. 1979. Growth stages and distribution of dry matter, N, P and K in winter wheat. – *Agron. J.* 71: 391–397.
- Zee, S. Y. & O'Brien, T. P. 1970. A special type of tracheary element associated with "xylem discontinuity" in the floral axis of wheat. – *Aust. J. Biol. Sci.* 23: 783–91.
- & O'Brien, T. P. 1971. Vascular transfer cells in the wheat spikelet. – *Aust. J. Biol. Sci.* 24: 35–49.

Edited by A. Kylin

III. Growth and accumulation of N , K^+ , Ca^{2+} and Mg^{2+} in barley exposed to various nutrient regimes and root/shoot temperatures

Paul Jensén and Harald Perby

Jensén, P. and Perby, H. 1986. Growth and accumulation of N , K^+ , Ca^{2+} and Mg^{2+} in barley exposed to various nutrient regimes and root/shoot temperatures. - *Physiol. Plant.* (In press).

Six cultivars of spring barley (*Hordeum vulgare* L. cvs Salve, Nürnberg II, Bomi, Risø 1508, Mona and Sv 73 608) were grown in water culture for three weeks with various combinations of mineral supply and differential root/shoot temperatures during the growth period. Most important for growth and accumulation of N , K^+ , Ca^{2+} and Mg^{2+} was the mineral supply, followed by the root temperature and the choice of cultivar. Treatments with low mineral supply or low root temperature induced a uniform reduction in growth and accumulation of the ions studied. The effects of low mineral supply and low root temperature on growth and N accumulation was additive, which indicates that these factors exert their influence independently of each other.

Roots grown at $10^{\circ}C$ were smaller and $Rb^+(^{86}Rb)$ influx was higher than in roots grown at $20^{\circ}C$. It is suggested that the control of $Rb^+(^{86}Rb)$ influx is af-

ected by the root temperature and the age of the plants.

The higher $^{86}\text{Rb}^+$ influx into the low temperature roots could not compensate for the smaller root size. However, the lower total mineral accumulation made up for the needs of the smaller plants and cannot explain the reduction in growth.

Additional key words - Age, allosteric regulation, cultivar, Rb^+ influx.

P. Jensén and H. Perby (reprint request), Dept. of Plant Physiology, Univ. of Lund, P.O. Box 7007, S-220 07 Lund, Sweden.

Introduction

In the laboratory, temperate cereals often encounter considerably higher temperatures than in the field. For convenience, shoots and roots of such plants are also kept at the same temperature. Clarkson (1976) questioned whether results obtained with plants cultivated at a high and uniform temperature reflect the physiology of field-grown plants. Temperate plants adapt to low soil temperatures, but shoot and root growth decrease (Power et al. 1967, Mack and Finn 1970, Moraghan and Porter 1975, Cumbus and Nye 1982, Smakman and Hofstra 1982) and roots become thicker with fewer laterals (Nye and Tinker 1977, Clarkson and Warner 1979, Cumbus and Nye 1982, Abbas-al-Ani and Hay 1983). More realistic growth conditions can be obtained with systems which maintain diffe-

rent shoot and root temperatures (Cooper et al. 1960, Mack and Barber 1960, Willis et al. 1963, Kemp 1972, Stone and Taylor 1982).

Ion uptake by roots adapted to temperatures in the range of 18 to 28°C decreased after transfer to lower temperatures (Carey and Berry 1978, Schimansky 1981). However, ion uptake is usually higher in roots adapted to about 8 to 15°C, compared with roots kept at temperatures around 20°C (Clarkson et al. 1974, Clarkson 1976, Deane-Drummond and Glass 1983, Siddiqi et al. 1984). The higher ion uptake is thought to be due to an increased number of carrier entities for active transport. $V_{\max}$ for K^+ (^{86}Rb) uptake in plants grown at 20°C increased after adaptation to 10°C, while K_m was about the same or increased slowly. In roots initially kept at 20°C, elements were fed to the xylem at a higher rate after adaptation to 12°C.

With regard to the relationships discussed, it becomes of interest for applied plant science to analyze the reactions of different cultivars under conditions that are reasonably close to what occurs in practical agriculture. In the present investigation the combined effects of variations in root/shoot temperature and mineral supply on growth, accumulation of N, K^+ , Ca^{2+} and Mg^{2+} and influx of Rb^+ (^{86}Rb) into the roots are compared for one-, two- and three-week-old barley plants. Since data for six cultivars is pooled in this paper, the influence of cultivar differences on variation in growth and mineral nutrition will be compared with the effects

of the growth temperature and mineral supply.

Abbreviations - DNP, 2,4-dinitrophenol.

Materials and methods

The plant material included six cultivars of spring barley (*Hordeum vulgare* L). Mona, Salve and Bomi have been cultivated in Scandinavia. Sv 73 608 and Risø 1508 are high-lysine lines derived from Mona and Bomi, respectively. Nürnberg II originates from a 19th century German land race.

Germination took place in darkness at ca 20°C in Petri dishes on filter papers moistened with distilled water. After three days, the seedlings were transferred to black plastic discs, 35 mm in diameter, each containing 10 plants. Four such plant groups were grown together in 2 l black-painted glass beakers containing 1.8 l nutrient medium.

The plants were grown on a complete nutrient medium and in 10 and 100 times dilutions of it. The full strength medium was composed of: 2.0 mM KNO₃, 1.0 mM Ca(NO₃)₂, 1.0 mM MgSO₄, 1.0 mM KH₂PO₄, 0.5 mM Na₂HPO₄, 0.1 mM Fe-EDTA, 1.5 μM MnSO₄, 0.25 μM ZnSO₄, 0.25 μM CuCl₂, 0.04 μM Na₂MoO₄, 10.0 μM H₃BO₃; pH was initially 6.1. The nutrient solutions were changed three times a week and always on the day before harvest. They were continuously aerated. Water losses from the beakers were compensated for by daily additions of distilled water.

The plants were placed in climate chambers with continuous light provided by General Electric F 48 power

groove 17-CVX 110 W fluorescent lamps, giving an irradiance of ca 25 W m^{-2} on the shoots. Air temperature was kept at 10, 15 or 20°C . For some treatments, the temperature around the roots (10°C) was regulated by the equipment shown in Fig. 1. The designs of experiments A and B are included in Figs 2 and 3.

In experiment A, uptake experiments were performed 7, 14 and 21 days after the transfer of seedlings to the nutrient media. For both shoots and roots the temperature regime was the same as during the preceeding week. Two plant groups were placed in each 2 l black-painted glass beaker containing 1.8 l $^{86}\text{Rb}^{+}$ -labelled nutrient medium with the same composition as the full strength medium except that the 2 mM KNO_3 was replaced by 1 mM RbNO_3 . The specific activity was ca 0.75 MBq l^{-1} for $^{86}\text{Rb}^{+}$. After 60 min the roots were rinsed for ten min in 1.8 l of unlabelled medium with the same composition as the radiolabelled medium. The roots were blotted between filter papers, and roots and shoots were separated and weighed for fresh weights. Contents of K^{+} , Ca^{2+} and Mg^{2+} were determined by atomic absorption spectrophotometry after digestion of the plant parts in a mixture of concentrated HNO_3 and HClO_4 (v/v 2:1). Radioactivity was determined by liquid scintillation counting.

In experiment B (Fig. 3), the plants were harvested after 7, 14 and 21 days and dried for two days at 70°C before determination of dry weights. N-contents were determined titrimetrically by an automatic Kjeldahl technique (Tecator Kjeltac 1003; Höganäs, Sweden), modi-

fied for efficient reduction of NO_3^- (98 -99 %; data not shown). The digestion procedure can be divided into four main steps:

- a. Samples (0.10 to 0.25g) are soaked and digested in 13 ml of a mixture of concentrated H_2SO_4 (1000 ml), concentrated H_3PO_4 (50 ml) and salicylic acid (50g).
- b. Reduction with Zn before digestion.
- c. The digestion temperature is raised to 350°C in 75 min, whereafter Hg-catalyst is added.
- d. A final digestion at 420°C for 40 min.

Results

General trends

Pooled data for up to three-week-old plants of the six barley cultivars are presented. For each combination of temperature/nutrient treatment, a general pattern was found for changes in fresh and dry weight and contents of K^+ , Ca^{2+} , Mg^{2+} and N (Figs 2 and 3).

Seedlings grown at 10°C the first week produced during this period less fresh and dry weight than seedlings grown at 20°C (Figs 2 and 3; treatment II and III vs I; VI vs V; VIII vs VII). When both root and shoot temperature increased stepwise on days 7 and 14 ($10 - 15 - 20^\circ\text{C}$), this effect was later compensated for (II vs I). When only the shoot temperature increased stepwise ($10 - 15 - 20^\circ\text{C}$) and the root was kept at 10°C , growth and accumulation of minerals were restricted (III vs I; VI vs V; VIII vs VII). Similarly, a limited mineral supply during the whole cultivation period, 21 days, or

a part of it, decreased growth and mineral contents of the plants (IV vs III; VII vs V; VIII vs VI). Growth and mineral accumulation decreased further when low root temperature and low mineral supply were combined (IV vs I and III; VIII vs V to VII).

Mineral levels

The effects of temperature and mineral supply on N levels in barley are shown in Fig. 3. The N levels were in most cases somewhat higher in shoots than in roots. The highest N levels were found in plants grown in full strength medium and exposed to a stepwise increasing shoot temperature and root temperature of 10°C (VI); followed by plants grown in full strength medium and kept at 20°C (V). The lowest N levels were found in one- and two-week-old plants supplied with minerals at a stepwise increasing rate and cultivated at 20°C (VII). On day 21, after a week on full strength medium, the N levels in such plants approached that in other plants (VII vs V, VI and VIII). N levels in plants cultivated with stepwise increasing nutrient supply and shoot temperature and a constant root temperature of 10°C (VIII) were intermediate.

Independently of temperature regime, K^+ levels in shoots of plants grown in full strength medium were almost the same (Fig. 4; I to III). Root levels of K^+ in plants grown in full strength medium and kept at 20°C or at a stepwise increase in root and shoot temperature decreased slowly with increasing age (I and II). For plants grown continuously at a root temperature of 10°

(III and IV), K^+ levels in the roots were reduced by c. 50 % between days 7 and 14 (III and IV).

Ca^{2+} levels in shoots (Fig. 4) were highest in three-week-old plants grown at 20°C and in full strength medium (Fig. 4; I) followed by plants exposed to stepwise increasing temperature (II and IV). Comparatively low Ca^{2+} levels were found in roots of plants cultivated in full strength medium at 20°C (I vs II and III).

Compared with plants grown in full strength medium and exposed to the same temperature regime during three weeks, root levels of Mg^{2+} in plants grown in medium diluted ten times were lower, while shoot levels were about the same (Fig. 4; IV vs III). When both shoot and root temperature increased stepwise, the changes in levels of Mg^{2+} were irregular (II). In plants cultivated at 20°C, shoot levels of Mg^{2+} increased with time (I).

Rb^+ (^{86}Rb) influx

Influx of Rb^+ in 7-, 14- and 21-day-old barley roots was influenced by the cultivation conditions (Fig. 5). Mainly the DNP-sensitive component of influx was affected, and DNP-resistant influx was low. For all treatments, influx of Rb^+ per root increased between day 7 and 21. Depending on the cultivation procedure the increase was carried out in different ways (I to IV). For all plants root expansion was most important for increased total uptake, since influx of Rb^+ was almost constant or decreased between days 7 and 21 when calculated per g fresh weight (Figs 2 and 5).

Discussion

During the first three weeks, growth of spring barley is primarily controlled by mineral supply, closely followed by temperature (Figs 2 and 3). Compared with growth reductions caused by these external factors, cultivar variation in growth (indicated as SD for the six cultivars) is somewhat smaller. Properties of the individual barley cultivars included in these experiments are discussed in a subsequent paper (Perby and Jensen 1986).

Three-week-old plants grown in full strength medium and at either a stepwisely increasing (10 - 15 - 20°C) or a constant temperature of 20°C have almost the same fresh weights and mineral contents (Fig. 2; I and II). Growth reductions in treatments III and VI can, therefore, mainly be attributed to the low root temperature (cf Tachibana 1982). External factors regulating growth can be ranked in order of importance as follows: mineral supply > root temperature (10 and 20°C) > cultivar (Figs 2 and 3). This verifies the results of Mack and Finn (1970), who exposed clones of timothy to varying fertilizer, moisture and soil temperature conditions. The total yield of herbage was influenced in the order fertilizer > soil temperature (10 and 20°C) > soil moisture > clonal stock.

Increase in dry weight (dry weight at harvest minus dry weight day 0; dry weight on day 0 was ca 35 mg per seedling) for treatments V to VIII can be used to test the interaction between a moderate root temperature stress and a restricted mineral supply on growth and nitrogen accumulation (Fig. 3). Related to treatment V

(high temperature and mineral supply), values for dry weight accumulation on day 21 in VI (low root temperature) and VII (initial mineral stress) were $29 \pm 1\%$ and $23 \pm 2\%$, respectively. If there is no synergistic action of temperature and mineral stress, the expected value for their combined effect on dry weight accumulation in treatment VIII will be $7 \pm 1\%$. The real value was $5 \pm 2\%$. The difference is insignificant ($P > 0.1$). A similar calculation for N-accumulation gave the same result. This indicates that moderate root temperature stress and restricted mineral supply independently depress dry weight production and N-accumulation in young barley plants. Apart from this, low temperature during the first week of cultivation partly inhibits the development of stressing N-levels in one- and two-week-old seedlings by depressing growth. Consequently the demand for nitrogen decreases (Fig. 3; VIII vs VII).

Low root temperatures decrease growth of roots and shoots of barley and other chilling tolerant plants (Figs 2 and 3; treatment III vs I, VI vs V; Moraghan and Porter 1975, Clarkson and Warner 1979, Cumbus and Nye 1982, Smakman and Hofstra 1982). Abbas Al-Ani and Hay (1983) studied root expansion in four cereal species cultivated at root temperatures of 5, 15 and 25°C. Among barley roots of equal length those grown at the lowest temperature were somewhat thicker than the others. However, the increase in diameter was small and the authors assumed this to be of minor importance for mineral nutrition. The temperature also affects the morphology

of the root (Nye and Tinker 1977).

Barley roots adapt the fluidity of their membranes to the ambient temperature, changing the composition of phospholipids (Clarkson et al. 1980). Some ion carrier systems adapt to the root temperature (Clarkson et al. 1974, Clarkson 1976, Deane-Drummond and Glass 1983). In our experiments influx of Rb^+ (root fresh weight) $^{-1}$ in three-week-old plants grown in full strength medium is higher in roots grown at 10°C than in roots grown at higher temperatures (Fig. 5; III vs I and II). Since there are minor differences in K^+ -levels among the roots of these plants (Fig. 4; I to III), differences in allosteric regulation as well as in number of ion carriers might be involved (Clarkson 1976, Glass 1976, Jensen and Pettersson 1978, Siddiqi et al. 1984). Similarly, in perennial ryegrass with roots kept at 10 and 20°C, uptake of NH_4^+ , but not of NO_3^- , adapts to the root temperature (Clarkson and Warner 1979).

In the long run, uptake of minerals is depressed if the roots are continuously kept at low temperatures (Figs 2 and 3; III vs I, VI vs V). Although the roots adapted to 10°C absorb ions at high rates per unit root fresh weight, they are not able to compensate for the difference in size (Figs 2, 3 and 5). The long-term growth depression is caused by the moderate root temperature stress and not by lack of minerals. The background for decreased growth may be explained by the growth regulator balance which presumably is affected by the root temperature (Clarkson et al. 1974). In our experiments levels of N in one- and two-week-old plants

exposed to low root temperatures were usually higher than in plants kept at high root temperature (Fig. 3; VI vs V, VIII vs VII). In the case of Ca^{2+} and Mg^{2+} , levels of the elements varied greatly between different temperature treatments (Fig. 4), but in no case was severe stress of Ca^{2+} and Mg^{2+} induced at low root temperature. K^+ -levels, especially in the roots, were low in two- to three-week-old plants with roots kept at 10°C (Fig. 4; III and IV). However, they are not low enough to fully explain growth reduction caused by a moderate temperature stress. This view supports Tachibana (1982) who, when comparing growth of cucumber varieties at different root temperatures, claimed that suppression of mineral uptake is not the primary cause of growth reduction at low root temperatures. Watts (1972) found that low root temperature decreased the expansion of corn leaves by effects on the leaf meristematic region.

Jensén (1978) described how DNP-insensitive uptake of $\text{K}^+(\text{}^{86}\text{Rb})$ and $(\text{}^{35}\text{S})$ -sulphate increased in importance as wheat grown in water culture aged. This is also shown for one- to three-week-old plants of barley grown in full strength medium and kept at 20°C (Fig. 5; I). It means that while levels of K^+ in the roots are almost constant (Fig. 4; I), they affect the allosteric regulation system differently at different ages. On the contrary, DNP-sensitive Rb-influx is of great importance in three-week-old plants grown in full strength medium and exposed to low root temperature (Fig. 5; III). Maybe physiological ageing proceeds differently as an effect

of the cultivation technique, keeping the active uptake systems intact for a longer time in roots adapted to low temperatures.

Acknowledgements - The authors thank Mrs Lena Lundh and Miss Kajsa Hedlund for skilful technical assistance and Dr Janet Bornman for correcting the language. Seeds were kindly provided by Svalöf AB, Svalöv, Sweden. The work was supported by grants from the Swedish Council for Forestry and Agricultural Research and O.E. and Edla Johanssons Foundation.

References

- Abbas Al-Ani, M.K. & Hay, R.K.M. 1983. The influence of growing temperature on the growth and morphology of cereal seedling root systems. - J. Exp. Bot. 34:1720-1730.
- Carey, R.W. & Berry, J.A. 1978. Effects of low temperature on respiration and uptake of rubidium ions by excised barley and corn roots. - Plant Physiol. 61:858-860.
- Clarkson, D.T. 1976. The influence of temperature on the exudation of xylem sap from detached root systems of rye (*Secale cereale*) and barley (*Hordeum vulgare*). - Planta 132:297-304.
- & Warner, A.J. 1979. Relationships between root temperature and the transport of ammonium and nitrate ions by italian and perennial ryegrass (*Lolium multiflorum* and *Lolium perenne*). - Plant Physiol. 64:557-561.
- , Shone, M.G.T. & Wood, A.V. 1974. The effect of pre-

- treatment temperature on the exudation of xylem sap by detached barley root systems. - *Planta* 121:81-92.
- , Hall, K.C. & Roberts J.K.M. 1980. Phospholipid composition and fatty acid desaturation in the roots of rye during acclimatization of low temperature. Positional analysis of fatty acids. - *Planta* 149:464-471.
- Cooper, D.J., Neilsen, K.F., White, J.W. & Kalbfleisch, W. 1960. Note on an apparatus for controlling soil temperatures. - *Can. J. Soil Sci.* 40:105-107.
- Cumbus, I.P. & Nye, P.H. 1982. Root zone temperature effects on growth and nitrate absorption in rape (*Brassica napus* cv. Emerald). - *J. Exp. Bot.* 33:1138-1146.
- Deane-Drummond, C.E. & Glass, A.D.M. 1983. Compensatory changes in ion fluxes into barley (*Hordeum vulgare* L. cv. Betzes) seedlings in response to differential root/shoot growth temperature. - *J. Exp. Bot.* 34: 1711-1719.
- Glass, A.D.M. 1976. Regulation of potassium absorption in barley roots: An allosteric model. - *Plant Physiol.* 58:33-37.
- Jensen, P. 1978. Changes in ion transport in spring wheat during ontogenesis. - *Physiol. Plant.* 43:129-135.
- & Pettersson, S. 1978. Allosteric regulation of potassium uptake in plant roots. - *Physiol. Plant.* 42:207-213.
- Kemp, G.A. 1972. Water bath for germination and root development studies under various temperature combinations of soil and ambient air. - *Can. J. Plant Sci.* 52:677-679.
- Mack, A.R. & Barber, S.A. 1960. A bath for soil tempera-

- ture control in pot culture work. - Agron. J. 52:299.
- & Finn, B.J. 1970. Differential response of timothy clonal lines and cultivars to soil temperature, moisture and fertility. - Can. J. Plant Sci. 50:295-305.
- Moraghan, J.T. & Porter, O.A. 1975. Maize growth as affected by root temperature and form of nitrogen. - Plant Soil 43:479-487.
- Nye, P.H. & Tinker, P.B. 1977. Solute Movement in the Soil-Root System. - Blackwell Scientific Publications, Oxford. pp. 208-209. ISBN 0-632-09730-2.
- Perby, H. & Jensen, P. 1986. Variation in growth and accumulation of N, K^+ , Ca^{2+} and Mg^{2+} among barley cultivars exposed to various nutrient regimes and root/shoot temperatures. - Physiol. Plant. (In press).
- Power, J.F., Willis, W.O., Grunes, D.L. & Reichman, G.A. 1967. Effect of soil temperature, phosphorus, and plant age on growth analysis of barley. - Agron. J. 59:231-234.
- Schimansky, C. 1981. Die Aufnahme von ^{28}Mg , ^{86}Rb und ^{45}Ca durch Gerstenpflanzen bei unterschiedlichen Wurzeltemperaturen. - Z. Pflanzenernähr. Bodenk. 144: 356-365.
- Siddiqi, M.Y., Memon, A.R. & Glass, A.D.M. 1984. Regulation of K^+ influx in barley. Effects of low temperature. - Plant Physiol. 74:730-734.
- Smakman, G. & Hofstra, J.J. 1982. Energy metabolism of *Plantago lanceolata*, as affected by change in root temperature. - Physiol. Plant. 56:33-37.
- Stone, J.A. & Taylor, H.M. 1982. A water bath system to

observe temperature effects on taproot and lateral root development of plants. - Soil. Sci. Soc. Am. J. 46:1343-1345.

Tachibana, S. 1982. Comparison of effects of root temperature on the growth and mineral nutrition of cucumber cultivars and figleaf gourd. - J. Jpn Soc. Hortic. Sci. 51:299-308.

Watts, W.R. 1972. Leaf extension in *Zea mays*. II. Leaf extension in response to independent variation of the temperature of the apical meristem, of the air around the leaves and of the root-zone. - J. Exp. Bot. 23: 713-721.

Willis, W.O., Power, J.F., Reichman, G.A. & Grunes, D.L. 1963. Constant temperature water baths for plant growth experiments. - Agron. J. 55:200.

Figure legends

Fig. 1. Arrangement in climate chamber for cultivation of plants with shoots and roots at different temperatures in the interval 10 - 20°C. A, cooling unit (Thermofrig), alcohol bath and temperature regulator; B, polythene vessel, 40 l, with circulating distilled water; C, black-painted glass beaker, 2 l, with 1.8 l nutrient solution (six beakers per vessel); D, outlet; E, inlet; F, connection between vessels.

Fig. 2. Design of experiment A (top) and fresh weights and total contents of K^+ , Ca^{2+} and Mg^{2+} in shoots (circles) and roots (triangles) of barley (with one plant as a basis) exposed to four different nutrient and tempera-

ture treatments (I-IV) during three weeks. Temperature regime (T): upper figure represents shoot temperature and lower figure root temperature. Nutrient supply (NS): Double-lined area (treatments I to III) represents cultivation in full strength medium, and single-lined area (treatment IV) represents cultivation in the same medium diluted ten times. Fresh weights and ion contents are shown as mean values for six cultivars $\pm$ SD (vertical bars). The value for each cultivar is the mean of eight groups with ten plants in each.

Fig. 3. Design of experiment B (top) and fresh and dry weights, total contents and concentrations of N in barley exposed to four different nutrient and temperature treatments (V- VIII) during three weeks. White area represents cultivation in a full strength medium diluted 100 times. The value for each cultivar is the mean of four groups with ten plants in each. Otherwise as for Fig. 2.

Fig. 4. Levels of K^+ , Ca^{2+} and Mg^{2+} in barley exposed to four different nutrient and temperature regimes during three weeks. Otherwise as for Fig. 2.

Fig. 5. $Rb^+(^{86}Rb)$ influx in roots of one-, two- and three-week-old barley. The isotope was supplied for 1 h. Filled symbols indicate means for root controls, while unfilled symbols indicate means for roots exposed to 10^{-4} M DNP. The value for each cultivar is the mean of four groups with ten plants in each. Otherwise as for Fig. 2.

Fig. 1

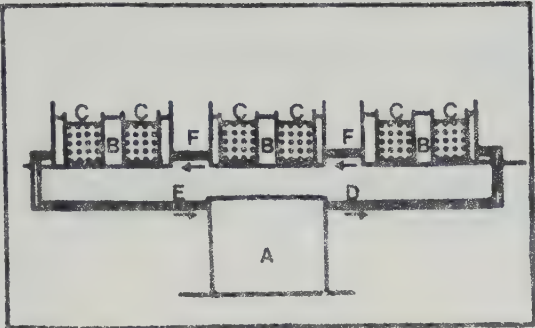


Fig. 2

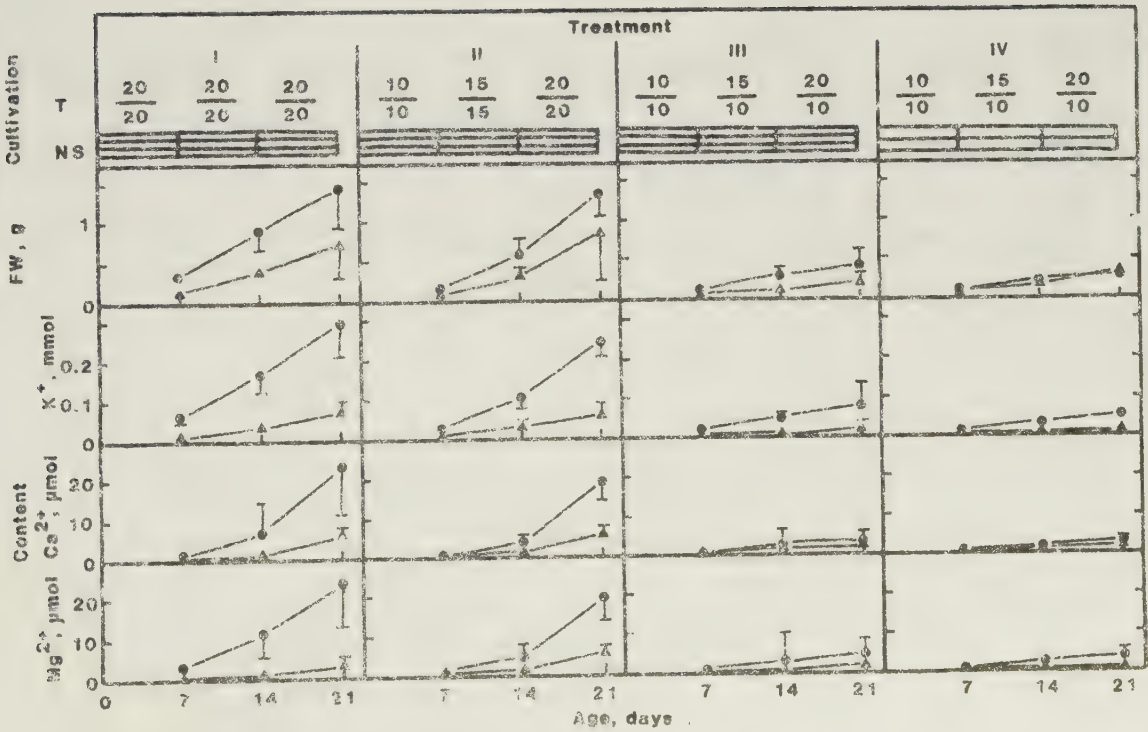


Fig. 3

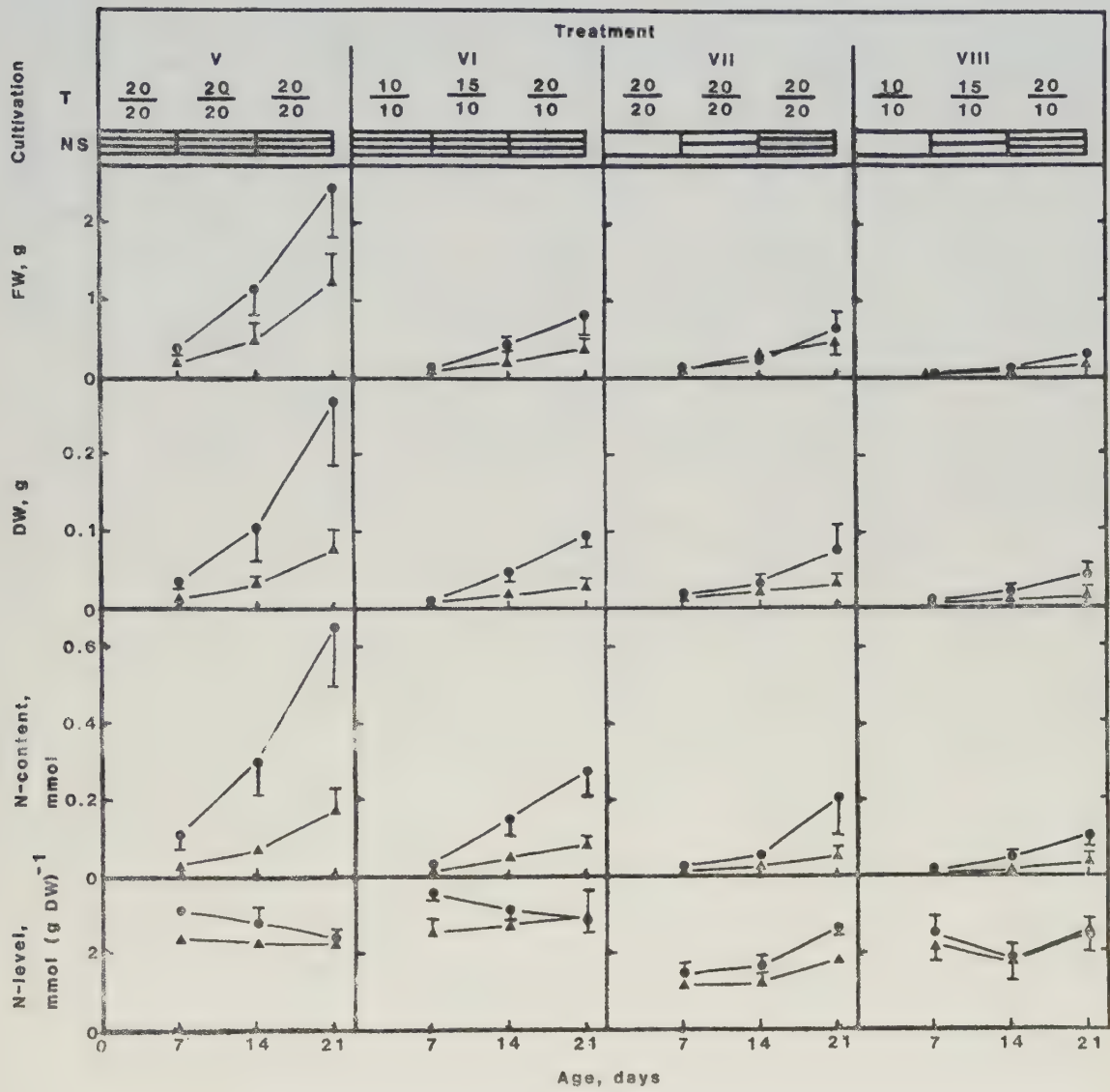


Fig. 4

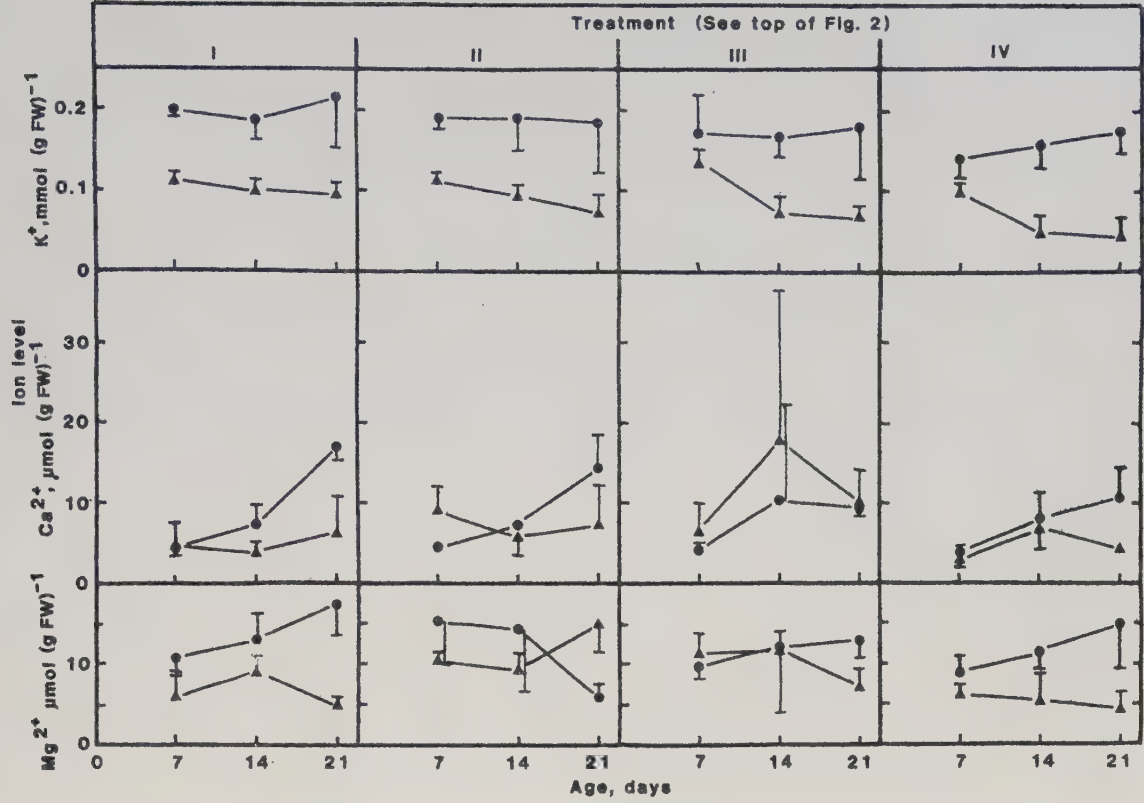
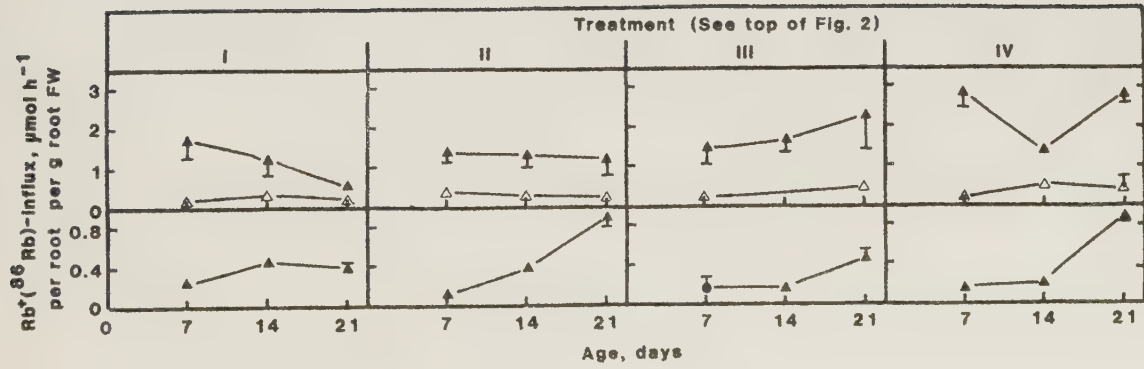


Fig. 5



IV. Variation in growth and accumulation of N , K^+ , Ca^{2+} and Mg^{2+} among barley cultivars exposed to various nutrient regimes and root/shoot temperatures

Harald Perby and Paul Jensen

Perby, H. and Jensen, P. 1986. Variation in growth and accumulation of N , K^+ , Ca^{2+} and Mg^{2+} among barley cultivars exposed to various nutrient regimes and root/shoot temperatures. -Physiol. Plant. (In press).

Six cultivars of barley (*Hordeum vulgare* L., cvs Salve, Nürnberg II, Bomi, Risø 1508, Mona and Sv 73 608) were exposed for three weeks to combinations of high and low mineral supply and differential root/shoot temperature. For all the parameters tested (fresh and dry weights, contents and levels of N , K^+ , Ca^{2+} and Mg^{2+} , and influx of Rb^+ (^{86}Rb)) the cultivar differences were influenced by the mineral supply, the root temperature and the age of the plants.

The cultivar differences in N nutrition of three-week-old plants could partly be attributed to variation in root size, uptake of N and in use-efficiency of the element. The cultivar variation in root-shoot partitioning of N was small, except when low mineral supply was combined with a low root temperature. Similarly, cultivar differences in contents of K^+ , Ca^{2+} and Mg^{2+} were influenced by variation in uptake, use-efficiency and root/shoot partitioning of the elements. Low root temperature increased cultivar

variation in K^+ , Ca^{2+} and Mg^{2+} partitioning.

The modern cultivar Salve was compared with Nürnberg II, which is derived from a German land race. Nürnberg II performed better than Salve when low root temperature and restricted mineral supply were combined. Otherwise Salve grew better, partly due to a more efficient use of N.

Two high-lysine lines, Risø 1508 and Sv 73 608, were compared with their mother lines Bomi and Mona. The differences obtained revealed no general effect of the high-lysine genes on growth and mineral nutrition of up to three-week-old barley plants.

Additional key words - High-lysine, land race, Rb^+ influx, use-efficiency.

H. Perby (reprint requests) and P. Jensén, Dept of Plant Physiology, Univ. of Lund, P. O. Box 7007, S-220 07 Lund, Sweden.

Introduction

Cultivar differences in mineral nutrition among crop species have been approached in several ways. Some studies have demonstrated the variation among barley cultivars in influx of elements, mainly K^+ (Schimansky and Marschner 1971, Pettersson 1978, Glass and Perley 1980, Jensén and Pettersson 1980, Glass et al. 1981, Siddiqi and Glass 1983a). V_{max} and K_m for K^+ influx depend on the age of the plants, the mineral regime and the cultivar (Siddiqi and Glass 1983b, Drew et al. 1984). Increa-

ses in $V_{\max}$ is supposed to be involved in hybrid and polyploid vigour (Clarkson and Hanson 1980). Pettersson (1978) showed that it is important to include estimates of cultivar differences in ion efflux in comparisons of flux rates.

Root-shoot transport of $K^+(^{86}Rb)$ varies among seedlings of barley cultivars (Jensén and Pettersson 1980). For older plants, the earliness of the cultivars influences the differences in root-shoot transport of $K^+(^{86}Rb)$ and $^{15}NO_3^-$ (Perby and Jensén 1984). Likewise, distribution in the shoots of K^+ and N and recently absorbed $K^+(^{86}Rb)$ and $^{15}NO_3^-$ in old plants of barley, varies among cultivars.

The genetic background of cultivar differences in use-efficiency of macro elements is known in some cases (Gabelman 1976, Gerloff 1976, Whiteaker et al. 1976, Gabelman and Gerloff 1982). Among cultivars of barley, Boken (1969, 1970) found considerable cultivar differences in use-efficiency of P on a whole plant basis, which changed with age.

Rasmusson et al. (1971) found that indoor and outdoor tests for cultivar differences in contents of macronutrients did not give the same result. This is not surprising, since adaptation to the ambient root and shoot temperatures occurs via many fundamental changes (Jensén and Perby 1986 and references therein). Bloom and Chapin (1981) found that when grown under identical conditions, a barley cultivar selected on cold soils had higher ammonium and nitrate influx rates at low concentrations and low temperatures than one selected on warm soils.

Mineral accumulation of figleaf gourd, *Cucurbita ficifolia*, and two cultivars of cucumber varied in sensitivity to low cultivation temperatures (Tachibana 1982).

In comparison with the influence of restricted mineral supply or a low root temperature, the cultivar differences in growth and mineral contents were smaller (Mack and Finn 1970, Jensen and Perby 1986). In practice, such differences in productivity are important. They demonstrate also genotypic variation in response to varying external conditions. In the present study the cultivar differences in some of the material presented by Jensen and Perby (1986) are analysed. The cultivars are grouped according to pairs; Nürnberg II, derived from a 19th century German land race, is compared with Salve, a modern cultivar with about the same earliness. The high-lysine lines Risø 1508 and Sv 73 608 are compared with their respective mother lines Bomi and Mona.

Materials and methods

Cultivars used in the experiments are shown in Tab. 1. The experiments and methods for determinations of elements have been described previously (Jensen and Perby 1986). The experiments are summarized in Fig. 1. Levels of significances were checked by a doublesided t-test.

Results

Reproducibility

Fresh and dry weights of three-week-old plants of six cultivars of barley are compared in pairs (Tabs 2 to 4).

If experiments A and B are compared, treatment V replicates I (plants grown in full strength medium and at 20°C; Fig. 1) and treatment VI replicates III (plants grown in full strength medium at a root temperature of 10°C and at a stepwise increasing shoot temperature). Cultivar differences were reproducible for Salve/Nürnberg II and Bomi/Risø 1508 (Tabs 2 and 3), but the levels of significance were not the same. For Mona and Sv 73 608 treatment VI gave the same principal result as III, while the outcome of treatment V differed from I (Tab. 4).

Development of cultivar differences

In plants kept at 20°C and grown in full strength medium, dry weights and N contents in one- and three-, but not two-week-old plants, were higher in Salve than in Nürnberg II (Tab 2b; treatment V). Among one-week-old seedlings grown in full strength medium and exposed to a uniform temperature of 10°C (VI), dry weight and N content were higher in Nürnberg II. After exposure to a stepwise increase in shoot temperature, dry weights of three-week-old seedlings were higher in Salve (Tab 2b; VI). Exposure to a stepwise increase in mineral supply and 20°C gave higher dry weights and N contents in two- and three-week-old plants of Salve (Tab. 2b; VII). The combination of a stepwise increase in shoot temperature and mineral supply and a root temperature of 10°C initially favoured Salve, but two weeks later Nürnberg II was superior (Tab 2b; VIII).

In one-, two- and three-week-old seedlings of Bomi

and Risø 1508 the most prominent change in cultivar differences occurred among seedlings cultivated in full strength medium with stepwise increase in shoot temperature and a root temperature of 10°C (data not shown). In two-week-old seedlings dry weight and N content were higher in Bomi, while the difference reversed during the third week of growth. When dry weights and N contents of Mona and Sv 73 608 differed significantly, the values for Mona were highest (data not shown). For these two cultivars the differences were rather consistent during the first three weeks.

A modern and an old cultivar

For three-week-old plants grown in ten times diluted medium with a root temperature of 10°C and stepwise increase in shoot temperature, shoot fresh weight of the 19th century cv. Nürnberg II was significantly higher (Tab. 2; IV). During the other experimental conditions (except VIII) the fresh weight was higher for Salve.

The contents of K^+ , Ca^{2+} and Mg^{2+} were significantly higher in three-week-old plants of Salve when cultivated in full strength medium at a root temperature of 10°C and a stepwise increase in shoot temperature (Tab. 2; III). The highest levels of N, Ca^{2+} and Mg^{2+} in shoots and roots and K^+ in roots of three-week-old plants were usually found in Nürnberg II. For three-week-old plants continuously grown in full strength medium, Rb^+ (^{86}Rb) influx per root was higher in Salve (I to III).

A late cultivar and its 'lys 3a'-mutant

Exposure to a stepwise increase in temperature gave

higher shoot fresh weight for plants of Bomi grown in full strength medium (Tab. 3: II). For three-week-old plants there were no significant differences in fresh weight of shoots, or in dry weight production, when mineral and temperature stress were combined (Tab. 3; IV and VIII). At two other treatments, Risø 1508 grew more vigorously than Bomi (I and VI). When contents of N, K^+ , Ca^{2+} and Mg^{2+} differed in three-week-old plants, they were highest in Risø 1508 (Tab. 3).

In three-week-old plants grown in full strength medium at 20°C, levels of K^+ in shoots and Mg^{2+} in roots were higher in Bomi (Tab. 3a; I). There was no difference in N-level (Tab 3b; V). In plants grown in full strength medium exposed to a stepwise increase in temperature, levels of K^+ , Ca^{2+} and Mg^{2+} in shoots and of K^+ in roots were significantly higher in Risø 1508 (II). Only levels of K^+ and N in the shoots were significantly higher in Risø 1508 when three-week-old plants grown in full strength medium of the two cultivars were compared at a root temperature of 10°C (III and VI) and a stepwise increase in shoot temperature. If the low root temperature was combined with restricted mineral supply, shoot levels of Ca^{2+} and Mg^{2+} were higher in Risø 1508, while no differences were obtained for the roots (IV). In shoots of three-week-old plants cultivated with stepwise increase in shoot temperature and mineral supply and a root temperature of 10°C, the N levels were higher in Bomi (Tab. 3b; VIII).

An early cultivar and its 'lys' back-cross

At four treatments there were several similarities in growth and mineral nutrition between three-week-old plants of Mona and its almost isogenic 'lys' back-cross Sv 73 608 (Tabs 1 and 4; I, II, IV and VIII). Otherwise, fresh and dry weights and contents of N, K^+ , Ca^{2+} and Mg^{2+} were higher in Mona (Tab. 4; III, V to VII).

In three-week-old plants grown in full strength medium, levels of N were higher in Sv 73 608 (Tab. 4b; V and VI), while N levels did not differ significantly after cultivation with a stepwise increase in mineral supply (VII and VIII).

If the roots of the plants were kept at 10°C, influx of Rb^+ , both per g root and per plant, were higher in Sv 73 608 (Tab. 4a; III and IV).

Discussion

Pattern of cultivar variation

Cultivar differences in N-nutrition among one-week-old seedlings of barley grown in full strength medium at 20°C can be explained by variation in relative growth rate (Chapin and Bielecki 1982), root size, and seed content and accumulation of N. Variation in use-efficiency and root/shoot partitioning of N are comparatively small (Perby and Jensen 1983). For three-week-old plants differences in levels of N (or its inverted value use-efficiency-ratio) are often significant, and depend on the mineral supply and the cultivation temperature (Tabs 2 to 4). As for younger plants, cultivar variation

in relative growth rate (Perby and Jensén 1986), root size and uptake of N are important among two-week-old plants; while cultivar differences in root/shoot partitioning of N are small in three cases out of four (Tab. 5).

Cultivar differences in content of K^+ , Ca^{2+} and Mg^{2+} of three-week-old barley are caused by variation in relative growth rate, and accumulation and use-efficiency of the elements (Tabs 2 to 4; Chapin and Bielecki 1982, Perby and Jensén 1983). There was no obvious relationship between the root size and the influx per plant of Rb^+ (^{86}Rb) ($P > 0.10$).

Low root temperatures decrease growth considerably but the effect varies between the cultivars (Tabs 2 to 4). Consequently, there are cultivar differences in the effect of low root temperature on demand for mineral nutrients (Jensén and Perby 1986). The cultivar differences in levels of N, K^+ , Ca^{2+} and Mg^{2+} were also influenced by the root temperature. Similarly, the size and structure of the roots vary between cultivars of barley and are affected by cultivation temperature and mineral supply (Tabs 2 to 4; Hackett 1968, Drew and Saker 1975, Nye and Tinker 1977, Jensén and Perby 1986). In Tab. 5, the SD is an expression of the size of the cultivar variation in root/shoot partitioning of dry matter and total plant content of N, K^+ , Ca^{2+} and Mg^{2+} . A root temperature of $10^{\circ}C$ gives rise to a larger cultivar variation in root/shoot partitioning of K^+ , Ca^{2+} and Mg^{2+} than a root temperature of $20^{\circ}C$ (III vs I).

For influx of K^+ and Rb^+ per root as well as per gram

root fresh weight, large cultivar differences exist (Pettersson 1978, Glass and Perley 1980, Glass et al. 1981, Jensén and Pettersson 1980, Siddiqi and Glass 1983a,b), which in some cases are affected by the treatment (Tabs 2 to 4). Similarly, NO_3^- influx varies between cultivars (H. Perby, unpublished results; Bloom and Chapin 1981). Seedlings of Salve, grown at 20°C , absorb Rb^+ at a higher rate than other cultivars, while Mona absorbs comparatively low amounts (Tabs 2a and 4a; Jensén and Pettersson 1980). Jensén and Pettersson (1980) found that the K^+ content in one-week-old seedlings of Salve was about the same as in some other cultivars, while efflux of K^+ from the roots was comparatively high. If three-week-old plants of Salve and Mona are compared, uptake of Rb^+ per g root fresh weight and per root are higher in Salve ($0.10 > P > 0.05$), while contents of K^+ are similar for treatments I, II and IV ($P > 0.10$) (Tabs 2a and 4a).

When effects of mineral supply and cultivation temperature on growth and mineral nutrition are summarized, it is evident that cultivars of barley respond differently to these factors. Additionally, the age of the plants and their cultivation properties influence the result of the comparisons (Tab. 2b; Sarič 1982, Perby and Jensén 1984). These observations have to be taken into account when screening for properties in mineral nutrition.

Comparisons of cultivars

The effects of modern plant breeding on the mineral phy-

siology of young barley plants are illustrated by Salve and Nürnberg II, a 20th and a 19th century cultivar with similar earliness (Tab. 1). Land races are usually adapted to low soil fertility and are, therefore, not very demanding. Their productivity is low (Harlan 1975, Ekman 1981). Consequently, Nürnberg II tolerates low root temperature combined with restricted mineral supply better than Salve (Tab. 2; IV and VIII). Under other external conditions, Salve grows significantly better and more N is absorbed per plant. In three-week-old plants, the levels of N are lower in the modern cultivar, which probably is an effect of a more efficient use of the element. In most cases this is also true for K^+ , Ca^{2+} and Mg^{2+} (Tab. 2).

High-lysine lines of barley might be of nutritional interest. Unfortunately, such lines, like Sv 73 608 and Risø 1508, yield less than their mother lines, although they are supposed to be almost isogenic (Tab. 1; Stoy and Bertholdsson 1981; N.O. Bertholdsson, R. Ekman and V. Stoy, personal communication). The high-lysine lines and their mother lines respond differently to K-fertilization (N.O. Bertholdsson, personal communication). Among three-week-old plants grown under various regimes, there are few indications of negative effects of the high-lysine genes on growth and mineral accumulation. Sv 73 608 seems to be more sensitive than Mona to the combination of high-salt conditions and a root temperature of $10^{\circ}C$. Under these conditions, Sv 73 608 accumulates less N and uses the element less efficiently than Mona, while the mutant uses K^+ more efficiently than Mona

(Tab. 4; III and VI). In contrast, Risø 1508 generally performs just as well as, or significantly better than Bomi during the first three weeks (Tab. 3). N-levels in the high-lysine lines are often higher than in their mother lines, reflecting a less efficient use of the element (Tabs 3b and 4b). Thus, no general negative effect of the high lysine genes 'lys' and 'lys 3a' can be distinguished for young barley plants. The drop in grain-yield is apparently due to factors located in the grains (Stoy and Bertholdsson 1984).

Acknowledgement - The authors thank Mrs Lena Lundh and Miss Kajsa Hedlund for skilful technical assistance and Dr. Janet Bornman for correcting the language. Seeds were kindly provided by Svalöf AB, Svalöv, Sweden. The work was supported by grants from the Swedish Council for Forestry and Agricultural Research and O.E. and Edla Johanssons Foundation.

References

- Bloom, A.J. & Chapin, F.S. 1981. Differences in steady-state net ammonium and nitrate influx by cold- and warm-adapted barley varieties. - Plant Physiol. 68:1064-1067.
- Boken, E. 1969. Nutrient concentration curves for oats and barley at different times of the period of growth. - Plant Soil 31:311-320.
- 1970. Studies on methods for determining varietal utilization of nutrients. II. Barley varieties and phos-

- phorus. - Plant Soil 33:645-652.
- Chapin, F.S. & Bielecki, R.L. 1982. Mild phosphorus stress in barley and a related low-phosphorus-adapted barleygrass: Phosphorus fractions and phosphate absorption in relation to growth. - Physiol. Plant. 54:309-317.
- Clarkson, D.T. & Hanson, J.B. 1980. The mineral nutrition of higher plants. - Annu. Rev. Plant Physiol. 31:239-298.
- Drew, M.C. & Saker, L.R. 1975. Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. - J. Exp. Bot. 26:79-90.
- , Saker, L.R., Barber, S.A. & Jenkins, W. 1984. Changes in the kinetics of phosphate and potassium absorption in nutrient-deficient barley roots measured by a solution-depletion technique. - Planta 160:490-499.
- Ekman, R. 1981. Biomass component studies in barley, their correlation to some yield characters and estimation of durable effect from 50 years of barley breeding. - In Barley Genetics IV. Proceedings of the Fourth International Barley Genetics Symposium (R.N.H. Whitehouse, ed.), pp 104-111. Edinburgh Univ. Press. ISBN 0-950-8016-0-7.
- Gabelman, W.H. 1976. Genetic potentials in nitrogen, phosphorus and potassium efficiency. - In Proceedings of Workshop on Plant Adaptation to Mineral Stress in

- Problem Soils (M.J. Wright, ed.), pp.205-212. National Agricultural Library, Beltsville, MD. November 22-23.
- & Gerloff, G.C. 1982. The search for, and interpretation of, genetic controls that enhance plant growth under deficiency levels of a macronutrient. - In Genetic Specificity of Mineral Nutrition of Plants (M.R. Saric, ed.), pp. 301-312. The Serbian Academy of Sciences and Arts, Belgrade.
- Gerloff, G.C. 1976. Plant efficiencies in the use of nitrogen, phosphorus and potassium. - In Proceedings of Workshop on Plant Adaptation to Mineral Stress in Problem Soils (M.J. Wright, ed.), pp. 161-173. National Agricultural Library, Beltsville, MD. November 22-23.
- Glass, A.D.M. & Perley, J.E. 1980. Varietal differences in potassium uptake by barley. - Plant Physiol. 65:160-164.
- , Siddiqi, M.Y. & Giles, K.I. 1981. Correlations between potassium uptake and hydrogen efflux in barley varieties. A potential screening method for the isolation of nutrient efficient lines. - Plant Physiol. 68:457-459.
- Hackett, C. 1968. A study of the root system of barley. I. Effects of nutrition on two varieties. - New Phytol. 67:287-299.
- Harlan, J.R. 1975. Our vanishing genetic resources. - Science 188:618-621.
- Jensén, P. & Pettersson, S. 1980. Varietal variation in uptake and utilization of potassium (rubidium) in

- high-salt seedlings of barley. - *Physiol. Plant.* 48:411-415.
- & Perby, H. 1986. Growth and accumulation of N, K⁺, Ca²⁺ and Mg²⁺ in barley exposed to various nutrient regimes and root/shoot temperatures. - *Physiol. Plant.* (In press).
- Mack, A.R. & Finn, B.J. 1970. Differential response of timothy clonal lines and cultivars to soil temperature, moisture and fertility. - *Can. J. Plant Sci.* 50: 295-305.
- Nye, P.H. & Tinker, P.B. 1977. *Solute Movement in the Soil-Root System.* - Blackwell Scientific Publications, Oxford. pp. 198-201 208-209. ISBN 0-632-09730-2.
- Perby, H. & Jensén, P. 1983. Varietal differences in uptake and utilization of nitrogen and other macro-elements in seedlings of barley, *Hordeum vulgare*. - *Physiol. Plant.* 58:223-230.
- & Jensén, P. 1984. Net uptake and partitioning of nitrogen and potassium in cultivars of barley during ageing. - *Physiol. Plant.* 61:559-565.
- & Jensén, P. 1986. Vegetative adaptation to N stress regimes in two barley cultivars with different N requirement. - *Plant Soil* (In press).
- Pettersson, S. 1978. Varietal differences in rubidium uptake efficiency of barley roots. - *Physiol. Plant.* 44:1-6.
- Rasmusson, D.C., Hester, A.J., Fick, G.N. & Byrne, I. 1971. Breeding for mineral content in wheat and bar-

- ley. - Crop Sci. 11:623-626.
- Sarič, M.R. 1982. Theoretical and practical approaches to the genetic specificity of mineral nutrition of plants. - In Genetic Specificity of Mineral Nutrition of Plants (M.R. Sarič, ed.), pp. 9-19. The Serbian Academy of Sciences and Arts, Belgrade.
- Schimansky, C. & Marschner, H. 1971. Suitability of Rb-86 as a tracer for potassium in studies relating to potassium uptake by maize, sugar beet and four varieties of barley. - Z. Pflanzenernähr. Bodenkd. 129: 141-147.
- Siddiqi, M.Y. & Glass, A.D.M. 1983a. Studies of the growth and mineral nutrition of barley varieties. I. Effect of potassium supply on the uptake of potassium and growth. - Can. J. Bot. 61:671-678.
- & Glass, A.D.M. 1983b. Studies of the growth and mineral nutrition of barley varieties. II. Potassium uptake and its regulation. - Can. J. Bot. 61:1551-1558.
- Stoy, V. & Bertholdsson, N.O. 1981. Yield formation in normal and high-lysine barley genotypes. - In Barley Genetics IV. Proceedings of the Fourth International Barley Genetics Symposium (R.N.H. Whitehouse, ed.), pp. 537-544. Edinburgh Univ. Press. ISBN 0-950-8016-0-7.
- & Bertholdsson, N.O. 1984. Assimilate production and incorporation into grain in normal and high lysine barleys. - In Cereal Grain Protein Improvement. Proceedings of the Final Research Co-ordination Meeting of the FAO/IAEA/GSF/SIDA Coordinated Research Programme on the use of Nuclear Techniques for Cereal

Grain Improvement. 6 to 12 December 1982. pp. 259-268. IAEA, Vienna. ISBN 92-0-111184-3.

Tachibana, S. 1982. Comparison of effects of root temperature on the growth and mineral nutrition of cucumber cultivars and figleaf gourd. - J. Jpn Soc. Hortic. Sci. 51:299-308.

Whiteaker, G., Gerloff, G.C., Gabelman, W.H. & Lindgren, D. 1976. Intraspecific differences in growth of beans at stress levels of phosphorus. - J. Am. Soc. Hortic. Sci. 101:472-475.

Tab. 1. Spring barley cultivars used in the experiments. Cultivars, except Nürnberg II, are classified according to earliness by G. Persson, Svalöf AB, Sweden (personal communication).

Cultivar	Main cultivation area	Type of cultivar
Mona	South Sweden	Early
Sv 73 608	None	Derived from Mona, carries 'lys'
Salve	Central Sweden	Fairly late
Nürnberg II	Germany	Variety from about 1833
Bomi	Denmark	Late
Risø 1508	None	Derived from Bomi, carries 'lys 3a'

Tab. 2a. Comparisons between a 19th (Nürnberg II=N) and a 20th (Salve=S) century fairly late cultivar of barley grown for three weeks at different nutrient and temperature regimes. Roman numerals refer to treatments according to Fig. 1 and Jensen and Perby (1986). Fresh weights are given as g (plant)⁻¹, contents as $\mu\text{mol plant}^{-1}$, levels of elements as $\mu\text{mol (g FW)}^{-1}$, influx of $\text{Rb}^+(\text{}^{86}\text{Rb})$ as $\mu\text{mol (g root FW)}^{-1} \text{ h}^{-1}$ and $\mu\text{mol (root)}^{-1} \text{ h}^{-1}$. Level of significance (Student's t-test) are indicated by stars: $^{\circ} 0.1 > P > 0.05$, * $0.05 > P > 0.01$ and ** $P < 0.01$. Values are means of eight replicates.

Parameter	Cultivar	Treatment			
		I	II	III	IV
FW, shoot	S	1.60 **	1.79 **	0.59 **	0.27
	N	1.28	1.31	0.38	0.35 **
	S	0.86 **	0.71	0.32 **	0.33
	N	0.61	0.88 **	0.21	0.35
Total K ⁺	S	407 **	304	142 **	58
	N	304	303	91	72 **
Total Ca ²⁺	S	28.0	27.9	9.0 **	5.2
	N	29.0	26.0	6.4	5.6
Total Mg ²⁺	S	30.0	27.1	10.5 **	6.3
	N	27.5	25.7	7.0	7.6
K ⁺ -level shoot	S	230 **	147	205	179
	N	183	182 *	205	174
	S	96	63	51	31
	N	103	74 *	66 $^{\circ}$	33
Ca ²⁺ -level shoot	S	16.8	11.7	9.7	11.0
	N	19.6 *	15.3 **	10.0	12.2 *
	S	4.8	9.7 **	10.2	4.5
	N	6.9 **	5.8	12.5 *	4.2
Mg ²⁺ -level shoot	S	18.8	12.8	14.0	17.3
	N	19.1	16.2 **	14.0	17.3
	S	4.4	6.2	7.0	4.9
	N	5.3 **	5.4	8.2 $^{\circ}$	4.9
Rb ⁺ -influx (g root FW) ⁻¹	S	0.72	1.93 **	2.41	3.01
	N	0.63	0.99	2.49	3.58 *
	S	0.62 **	1.36 **	0.78 **	0.99
	N	0.38	0.87	0.53	1.24

Tab. 2b. Comparisons between one-, two- and three-week-old plants of Nürnberg II (N) and Salve (S) grown at different nutrient and temperature regimes (see Fig. 1). Dry weight given as mg (plant)^{-1} , total N-contents as $\mu\text{mol (plant)}^{-1}$ and N levels as mmol (g DW)^{-1} . Values are means of four replicates. Otherwise as for Tab 2a.

Para- meter	Culti- var	Treatment			
		V	VI	VII	VIII
FW	day 21 shoot	S 2.59 **	0.83	0.84	0.34
		N 2.15	0.80	0.65	0.32
	root	S 1.31 **	0.39 **	0.52	0.15
		N 1.06	0.31	0.48	0.28 **
DW,	day 7	S 59 **	16	33	13 **
		N 48	18 **	34	9
	day 14	S 122	72	66 **	34
		N 131	69	47	41 **
	day 21	S 405 **	130 **	136	61
		N 301	118	107	71 *
	Total N day 7	S 178 **	50	43	30 **
		N 142	57 **	48	22
	day 14	S 329	221	91 **	66
		N 385 *	215	70	72
	day 21	S 922 *	376	337 °	149
		N 761	365	263	190 **
N-level	day 7 shoot	S 3.21	3.63	1.37	2.69 **
		N 3.15	3.64	1.55 *	2.52
	root	S 2.46	2.56	1.18	2.01
		N 2.36	2.69 **	1.19	2.18 **
	day 14 shoot	S 2.80	3.19	1.57	2.07 **
		N 3.08 **	3.29 °	1.65	1.74
	root	S 2.80	2.74	1.09	1.61
		N 2.41	2.66	1.23 **	1.77 **
	day 21 shoot	S 2.29	2.83	2.74	2.49
		N 2.57 **	3.09 **	2.74	2.67 *
	root	S 2.23	3.11	1.76	2.30
		N 2.38 °	3.11	1.77	2.67 **

Tab. 3a. Comparisons between a late cultivar (Bomi=B) and its 'lys 3a' mutant (Risø 1508=R) grown for three weeks at different nutrient and temperature regimes (see Fig. 1). Otherwise as for Tab 2a.

Para- meter	Culti- var	Treatment			
		I	II	III	IV
FW shoot	B	1.38	1.51 **	0.34	0.27
	R	1.78 **	1.20	0.42 °	0.27
	B	0.66	1.04	0.16	0.26
	R	1.00 **	0.93	0.23 °	0.34 *
Total K ⁺	B	352	325	75	58
	R	432 *	312	101 *	59
Total Ca ²⁺	B	28.4	26.0	5.2	3.3
	R	36.4 **	26.0	6.0	4.6 **
Total Mg ²⁺	B	28.4	28.0 °	6.1	4.6
	R	36.0 *	24.1	7.3	5.8 *
K ⁺ -level shoot	B	214 *	175	151	164
	R	194	202 **	194 *	164
	B	88	59	79	49
	R	89	76 **	82	44
Ca ²⁺ -level shoot	B	17.0	13.4	9.5	8.2
	R	17.2	16.5 **	9.0	11.5 **
	B	7.2°	5.6	9.7	4.2
	R	5.9	6.4	10.7	4.2
Mg ²⁺ -level shoot	B	17.9	14.8	13.2	12.3
	R	17.5	16.2 **	12.3	15.6 **
	B	5.7 **	5.3	7.1	4.9
	R	4.9	5.1	8.2	4.9
Rb ⁺ -influx B g root FW ⁻¹	B	0.46	1.12	1.82 °	2.93 °
	R	0.51	0.81	1.35	2.65
	B	0.30	1.16	0.29	0.76
	F	0.51 **	0.75	0.31	0.90 **

Tab. 3b. Comparisons between three-week-old plants of Bomi (B) and Risø 1508 (R) grown at different nutrient and temperature regimes (see Fig. 1). Otherwise as for Tab. 2a and b.

Para- meter	Culti- var	Treatment				
		V	VI	VII	VIII	
FW	shoot	B	2.64	0.82	0.58	0.30
		R	2.80	0.97 **	0.62 °	0.30
	root	B	1.34	0.34	0.43	0.14 °
		R	1.36	0.47 **	0.48 °	0.13
DW	B	368	130	96	53	
	R	378	143 *	100	59	
Total N	B	877	357	223	134	
	R	901	413 **	239 *	129	
N-level	shoot	B	2.42	2.73	2.56	2.49 **
		R	2.43	2.90 **	2.69 *	2.10
	root	B	2.26	2.80	1.79	2.61
		R	2.23	2.85	1.75	2.47

Tab. 4a. Comparisons between an early cultivar (Mona=M) and its 'lys' back-cross (Sv 73 608=Sv) grown for three weeks at different nutrient and temperature regimes (see Fig. 1). Otherwise as for Tab. 2a.

Para- meter	Culti- var	Treatment			
		I	II	III	IV
FW shoot	M	1.21	1.12	0.45 **	0.24
	Sv	1.24	1.15	0.28	0.26
root	M	0.57	0.51	0.20 **	0.29
	Sv	0.64	0.76 **	0.14	0.28
Total K ⁺	M	345	261	92 **	58
	Sv	353	304	64	63
Total Ca ²⁺	M	23.0	22.0	5.7 **	3.6
	Sv	23.0	22.0	4.0	3.8
Total Mg ²⁺	M	21.8	20.7	6.9 °	4.1
	Sv	21.9	21.7	5.1	4.6
K ⁺ -level shoot	M	237	196	171 *	179
	Sv	237	208	155	184
root	M	103	85	77 **	56
	Sv	100	86	46	51
Ca ²⁺ -level shoot	M	15.9	15.5	8.2	10.2
	Sv	15.4	13.7	9.0	10.0
root	M	6.8 °	9.9 °	9.7	4.0
	Sv	6.0	7.7	8.0	4.2
Mg ²⁺ -level shoot	M	15.6	15.6	11.9	13.2
	Sv	15.6	14.6	12.3	13.6
root	M	5.4 **	6.9	7.4 **	3.3
	Sv	4.6	6.6	5.4	3.3
Rb ⁺ -influx g root FW ⁻¹	M	0.52	1.42 **	1.75	2.09
	Sv	0.42	0.71	3.66 **	2.90 **
root ⁻¹	M	0.30	0.73 **	0.35	0.60
	Sv	0.27	0.54	0.50 **	0.82 **

Tab. 4b. Comparisons between three-week-old plants of Mona (M) and Sv 73 608 (Sv) grown at different nutrient and temperature regimes (see Fig. 1). Otherwise as for Tabs 2 a,b and 4a.

Para- meter	Culti- var	Treatment			
		V	VI	VII	VIII
FW	shoot	M 2.31 ^o	0.88 **	0.68 *	0.31
		Sv 2.26	0.64	0.55	0.27
	root	M 1.30 **	0.39 **	0.52 *	0.15
		Sv 1.03	0.27	0.35	0.13
DW	M	336 *	129 **	114 **	55
	Sv	290	98	88	49
Total N	M	774	357 **	274 **	138 ^o
	Sv	742	293	215	119
N-level	shoot	M 2.33	2.81	2.66	2.48 ^o
		Sv 2.59 **	2.99 **	2.65	2.36
	root	M 2.21	2.62	1.78	2.58
		Sv 2.44 **	2.98 **	1.90	2.63

Tab. 5. Dry weights and contents of N, K⁺, Ca²⁺ and Mg²⁺ in roots as percentage of total in three-week-old plants of barley. Treatment according to Fig. 1. Values are means for six cultivars (eight replicates each for treatments I to IV and four for V to VIII) ± SD.

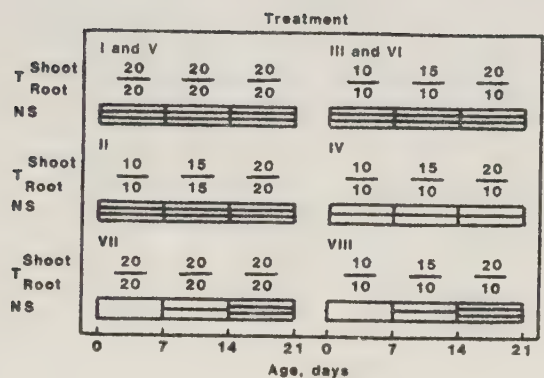
Parameter	Treatment			
	I	II	III	IV
K ⁺	19 [±] ₂	19 [±] ₃	18 [±] ₇	22 [±] ₅
Ca ²⁺	16 [±] ₂	24 [±] ₂	35 [±] ₆	32 [±] ₅
Mg ²⁺	13 [±] ₁	19 [±] ₃	27 [±] ₁₀	24 [±] ₃
	V	VI	VII	VIII
DW	22 [±] ₁	23 [±] ₂	29 [±] ₂	24 [±] ₁
N	21 [±] ₁	23 [±] ₂	22 [±] ₂	26 [±] ₄

Figure legend

Fig. 1. Design of treatments I - VIII. T temperature; NS nutrient supply. Double-lined area indicates cultivation on full strength medium (=100 %) 2.0 mM KNO₃, 1.0 mM Ca(NO₃)₂, 1.0 mM MgSO₄, 1.0 mM KH₂PO₄, 0.5 mM Na₂HPO₄, 0.1 mM Fe-EDTA, 1.5 μM MnSO₄, 0.25 μM ZnSO₄, 0.25 μM CuCl₂, 0.04 μM Na₂MoO₄, 10.0 μM H₃BO₃. pH was initially 6.1. Single-lined and unlined areas indicate cultivation on 10 and 1 % of the full strength medium, respectively. Plants were harvested on days 7, 14 and 21. For

treatments I to IV, $\text{Rb}^+(\text{}^{86}\text{Rb})$ influx was determined during 60 min followed by a 10 min rinse of the roots in inactive medium. In the uptake solution, 2 mM KNO_3 was replaced by 1 mM $\text{Rb}^+(\text{}^{86}\text{Rb})\text{NO}_3$. After harvest, fresh weight and contents of K^+ , Ca^{2+} and Mg^{2+} were determined. For treatments V to VIII fresh and dry weights and content of N were determined. For more details, see Jensen and Perby (1986).

Fig. 1



Va. Vegetative adaptation to N stress regimes in two barley cultivars with different N requirement.

HARALD PERBY and PAUL JENSEN

Department of Plant Physiology, P.O. Box 7007, S-220 07
Lund, Sweden.

Key words: Barley Cultivar Main stem N requirement
N stress Partitioning Tiller Vegetative adaptation

Summary: Plants of two barley cultivars, differing in requirement for N, were grown on water culture at combinations of stressing and non-stressing rates of N supply. At all N regimes, Kajsa, the cultivar with the lowest N requirement, produced more dry matter and used N more efficiently than Hellas. For both cultivars the morphological development was strongly influenced by the N supply, mainly visualized as effects on tillering. At N stress, tillering was more inhibited for Kajsa than for Hellas. At higher rates of N supply Kajsa formed fewer, but in average large tillers than Hellas.

Introduction

Cultivar variation in mineral nutrition of barley has mainly been related to genetic variation in basic processes involved in mineral physiology (for references, see¹⁰), while the influence of morphological differences has received less attention. The structure and the size of the roots vary between cultivars^{7, 10}. Tillering is important for the vegetative development of cereal

shoots¹. The rate of this process is influenced by the supply of N and the choice of cultivar², ¹². Cereals adapt to high or low mineral supply by regulating tillering. Plants with few tillers and a low growth rate survive under mineral stress³, whereas plants with many tillers and a high growth rate grow vigorously on large mineral resources.

In the present essay, vegetative development, dry matter production and N accumulation are compared for two cultivars of barley. Developmental changes were correlated with adaptation to low-N treatments.

Methods: The experiment was performed with two cultivars of barley (*Hordeum vulgare* L.). Hellas, a fairly late cultivar, has been grown in south Sweden and Kajsa, a very early cultivar, in north Sweden. In the field, Hellas require more N than Kajsa (G. Persson, Svalöf AB, Sweden, personal communication).

Seeds of both cultivars were imbibed at 10°C in distilled water for one day. They were germinated on moist filter papers in petri dishes for two and a half days at 20°C. The seedlings were transferred to black plastic discs, 35 mm in diameter. Two discs with three seedlings each were placed together in a 2 l black-painted beaker containing 1800 ml nutrient medium.

The standard medium was composed of 1.6 mM KNO₃, 0.8 mM Ca(NO₃)₂, 0.8 mM MgSO₄, 0.8 mM KH₂PO₄, 0.4 mM Na₂HPO₄ and 0.16 mM Fe-EDTA. The concentrations of micronutrients (except Fe) were 80 percent of those recommended⁸. Initial pH was ca 6.1. Plants were grown at two other

NO_3^- concentrations: 10% and 2.5% of the NO_3^- concentration in the standard medium. The remainder of the NO_3^- was then replaced by SO_4^{2-} . The nutrient solutions were continuously aerated and replaced every fourth day. Water levels in the beakers were adjusted daily with distilled water. The design of the experiment is shown in Fig. 1.

The plants were kept in a greenhouse. Sunlight was complemented with mercury lamps (Philips 400W, total irradiance $80\text{--}90 \text{ Wm}^{-2}$). The daylength was 16 h. The temperature was $16 \pm 2^\circ\text{C}$ and relative humidity ca 65 percent.

The appearance of leaves on the main stem and the start of tillering were followed. Six plant groups of each cultivar and treatment were harvested after 16, 28 and 52 days. 16-day-old plants were divided into shoots and roots. On older plants tillers were counted, whereafter roots, main stems, tillers and, if present, ears were separated¹. Dry leaves on the oldest plants were not separable and were included in the main stem fraction. The introduced error is negligible¹¹. The plant parts were dried at 60°C for two days before determination of dry weights. Total contents of N were determined by an automatic Kjeldahl technique modified⁹ for efficient reduction of NO_3^- .

Results

Vegetative development

Plants of both cultivars given the highest NO_3^- supply developed eight leaves on the main stem (10% - S; Tab. 1). At other combinations of NO_3^- supply before and after

day 16 only seven leaves developed on the main stem. A low N supply during any part of the cultivation period delayed expansion of leaves thereafter, Hellas generally being somewhat behind Kajsa. Similarly, tillering was delayed among plants supplied 2.5% medium the first 16 days. The number of vital tillers on 28- and 52-day-old plants depended on the N supply before and after day 16. These differences were significant ($0.05 > P > 0.01$). Kajsa usually had fewer tillers than Hellas.

Dry weight and content of N

When treated equally from day 16, dry weight and N accumulation in 28- and 52-day-old plants were affected by the NO_3^- supply before day 16 (Figs 1 and 2). Similarly, the NO_3^- regime after day 16 greatly influenced growth and N accumulation. Kajsa generally grew better and accumulated in three cases of four more N than Hellas. Only in one case differed N contents significantly between Hellas and Kajsa (Tab. 2). For 52-day-old plants, cultivar differences in dry weight were always significant.

Compared with the plants receiving most N, dry weights of main stems and roots of 52-day-old plants were reduced by 10 to 55 percent if the plants were grown in 2.5% medium or in 10% medium before respectively after day 16 (Figs 1 and 3). The percentages of the dry matter and total N content (Figs 3 and 4) found in the roots were about the same in the two cultivars, but varied according to the NO_3^- supply. Dry matter and N accumulation in tillers on 52-day-old plants decreased with 90 to 99 percent if grown at 10% medium from day

16.

Levels of N

Levels of N (Fig. 5) increased between day 16 and 28 in plants transferred from 10% and 2.5% media to standard medium. For plants continuously supplied 10% medium, N levels in roots and main stems decreased as the plants aged. In plants supplied 2.5% medium initially and thereafter 10% medium, the N level in main stems increased between day 16 and 28, while it was almost constant in roots. In tillers, levels of N were usually higher than in main stems and roots. With one exception, the N levels in tillers decreased between day 28 and 52. While N levels in 16- and 28-day-old plants of Kajsa and Hellas were almost the same, N levels in 52-day-old plants were usually higher in Hellas.

Discussion

Determination of NO_3^- concentrations in used nutrient solutions with an ion selective electrode¹¹ showed that the standard medium supplied NO_3^- to the plants at a non-stressing rate (data not shown). Seedlings nearly deplete the 10% medium for NO_3^- , and early growth decreases to some extent. If older plants are kept on 10% medium, N stress turns severe due to an increasing demand. The 2.5% medium induces severe N stress.

Growth rate of barley seedlings is lower when application of NO_3^- is delayed beyond unfolding of the first leaf^{4, 5, 6}. N stress before or after day 16 decreases dry weight production and N accumulation (Figs 1 and 2). The effect of the early NO_3^- supply is still notable on

day 52. Although N stress decreases the size of the main stem, the effect on tillers is more important (Figs 1 and 3). Under N stress, the plants strongly give priority to the main stem, in contrast to the situation at higher rates of NO_3^- supply (Figs 1 - 4). N levels are generally highest in tillers and lowest in roots (Fig. 5), a result of the more juvenile condition of the tillers¹².

Kajsa produces more dry matter than Hellas at all rates of NO_3^- supply (Fig. 1 and Tab. 2). In three cases of four, Kajsa accumulates more N (Fig. 2 and Tab. 2). Among the oldest plants, N levels are usually lowest in Kajsa, indicating a more efficient use of the element. In 52-day-old plants supplied standard medium from day 16, dry matter and N are partitioned in the same manner in both cultivars (Figs 3 and 4). The inhibition of tiller growth, induced by severe N stress after day 16, is most prominent for Kajsa. Kajsa produces fewer, but on average larger tillers than Hellas (Figs 1 and 3, Tab. 1). Similar cultivar differences in tillering have been described^{2, 12}.

The nitrogen supply affects leaf emergence rate and the day for the start of tillering (Tab. 1). If there are any cultivar differences in this respect, very early Kajsa, is always ahead of fairly late Hellas.

In summary, the cultivar differences are best visualized by the oldest plants¹¹. The strategies for adaptation to N stress differ between cultivars. Kajsa, known to require less N supply on the fields, produces more

dry matter, and uses N more efficiently than Hellas (Figs 1 and 5). Differences in N accumulation is in three cases of four not significant (Tab. 2). Exposed to N stress Kajsa inhibits expansion of tillers more than Hellas (Fig. 3 and Tab. 1). If NO_3^- is supplied at a non-growth-limiting rate, tillers contribute to the biomass to the same extent in both cultivars. It can be concluded that differences in morphology contribute to the differences between these two barley cultivars in N nutrition.

Acknowledgement: We would like to thank Mr Fredrik Owman for skilful technical assistance and Prof. Terence Murphy for critical reading of the manuscript. The work was supported by grants from O.E. and Edla Johanssons Foundation, The Swedish Society for the Conservation of Nature and Hierta-Retzius Foundation.

References

1. Briggs, D.E. 1978. Barley. - Chapman and Hall Ltd, London. pp 14-19. ISBN 0-412-11870-X.
2. Cannell, R.Q. 1969. The tillering pattern in barley varieties. I. Production, survival and contribution to yield by component tillers. - J. Agric. Sci., Camb. 72:405-422.
3. Chapin, F.S. 1983. Adaptation of selected trees and grasses to low availability of phosphorus. - Plant Soil 72:283-287.
4. Dale, J.E. 1972. Growth and photosynthesis in the first leaf of barley. The effect of time of application of nitrogen. - Ann. Bot. 36:967-979.

5. -. 1976. Nitrate reduction in the first leaf and roots of barley seedlings grown in sand and in culture solution. - Ann. Bot. 40:1177-1184.
6. -, Felipe, G.M. & Marriott, C. 1974. An analysis of the response of young barley seedlings to time of application of nitrogen. - Ann. Bot. 38:575-588.
7. Hackett, C. 1968. A study of the root system of barley. I. Effects of nutrition on two varieties. - New Phytol. 67:287-299.
8. Hewitt, E.J. & Smith, T.A. 1975. Plant Mineral Nutrition. - The English Universities Press Ltd, London. p. 32. ISBN 0-340-05086-1.
9. Jensen, P. and Perby, H. 1986. Growth and accumulation of N, K⁺, Ca²⁺ and Mg²⁺ in barley exposed to various nutrient regimes and root/shoot temperatures. - Physiol. Plant. (In press).
10. Perby, H. & Jensen, P. 1983. Varietal differences in uptake and utilization of nitrogen and other macroelements in seedlings of barley, *Hordeum vulgare*. - Physiol. Plant. 58:223-230.
11. - & Jensen, P. 1984. Net uptake and partitioning of nitrogen and potassium in cultivars of barley during ageing. - Physiol. Plant. 61:559-565.
12. Thorne, G.N. 1962. Survival of tillers and distribution of dry matter between ear and shoot of barley varieties. - Ann. Bot. 26:37-54.

Tab. 1. Influence of NO_3^- supply on leaf emergence on main stem, emergence of first tiller and total number of vital tillers. Code left of hyphen indicates NO_3^- supply day 0 to 16 and right of hyphen supply day 16 to 52 (S=standard medium). H= Hellas and K= Kajsa. Times for emergence of leaves and tillers are given as the median for 54 (day 0 to 16), 36 (day 16 to 28) and 18 (day 28 to 52) plants per treatment and cultivar. F indicates flag leaf. Total number of vital tillers are given as means per plant $\pm$ SE. Leaves number 1 and 2 always emerged on day 0 and day 4, respectively.

NO ₃ ⁻ supply	Culti- var	Leaf number:							First tiller	Number of	
		3	4	5	6	7	8	vital tillers			
		day of emergence								day 28	day 52
10%-S	H	8	14	18.5	24	32	38 ^F	11	4.5±0.3	10.1±0.6	
	K	8	14	18.5	24	31	36 ^F	11	3.2±0.2	6.4±0.2	
10%-10%	H	8	14	19.5	27	37 ^F	-	11	2.8±0.4	3.3±0.3	
	K	8	14	19.5	26.5	32 ^F	-	11	1.8±0.2	0.4±0.2	
2.5%-S	H	11.5	18	23	30.5	35 ^F	-	21	1.9±0.3	5.9±0.5	
	K	11	18	22	28	34 ^F	-	20	2.2±0.3	5.2±0.4	
2.5%-10%	H	11.5	18	23	31	36.5 ^F	-	27	1.8±0.2	2.1±0.2	
	K	11	18	23	29	35 ^F	-	28	1.4±0.2	1.0±0.1	

Tab. 2. Dry weights and N contents of 52-day-old plants. Levels of significance for cultivar differences are indicated by stars, * $0.05 > P > 0.01$ and ** $P < 0.01$. Otherwise as for Tab. 1.

NO ₃ ⁻ supply	Culti- var	Dry weight g	N content mmol
10%-S	H	2.93	6.65
	K	4.80**	8.07
10%-10%	H	0.94	1.27
	K	1.52**	1.31
2.5%-S	H	1.70	5.16
	K	2.82**	6.36*
2.5%-10%	H	0.68	1.07
	K	0.93*	1.04

Figure legends

Fig. 1. Dry weight production per plant for two barley cultivars. Plants were cultivated with various NO_3^- supplies (NS). Standard medium= black area, 10% medium= dotted area and 2.5% medium= white area. Values are means for six plant groups with three plants each. SE was usually less than 8% of mean.

Fig. 2. Content of nitrogen in two barley cultivars. Treatments as in Fig. 1. SE was usually less than 5% of mean.

Fig. 3. Partitioning of dry matter between main stem, tillers, ears and root in two barley cultivars. Values are given as percent of total dry weight. Filled circles indicate main stem, unfilled circles tillers, filled triangles root and unfilled triangles ears.

Fig. 4. Partitioning of N between main stem, tillers, ears and root in two barley cultivars. Otherwise as for Fig. 3.

Fig. 5. N levels in main stems, tillers, ears and roots for two barley cultivars. Treatments as in Fig. 1. Symbols as in Figs 3 and 4. SE was usually less than 8% of mean.

Fig. 1

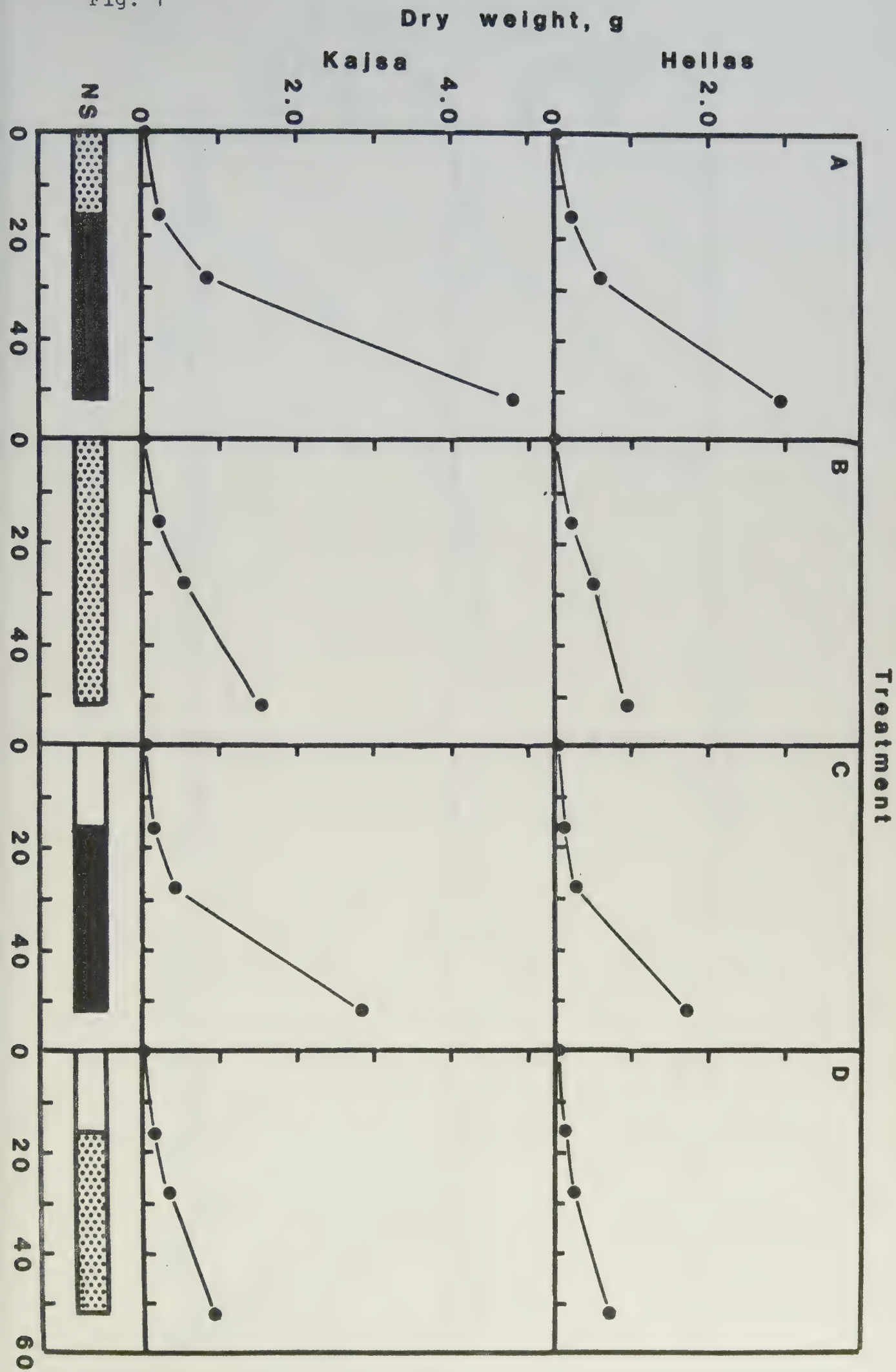


Fig. 2

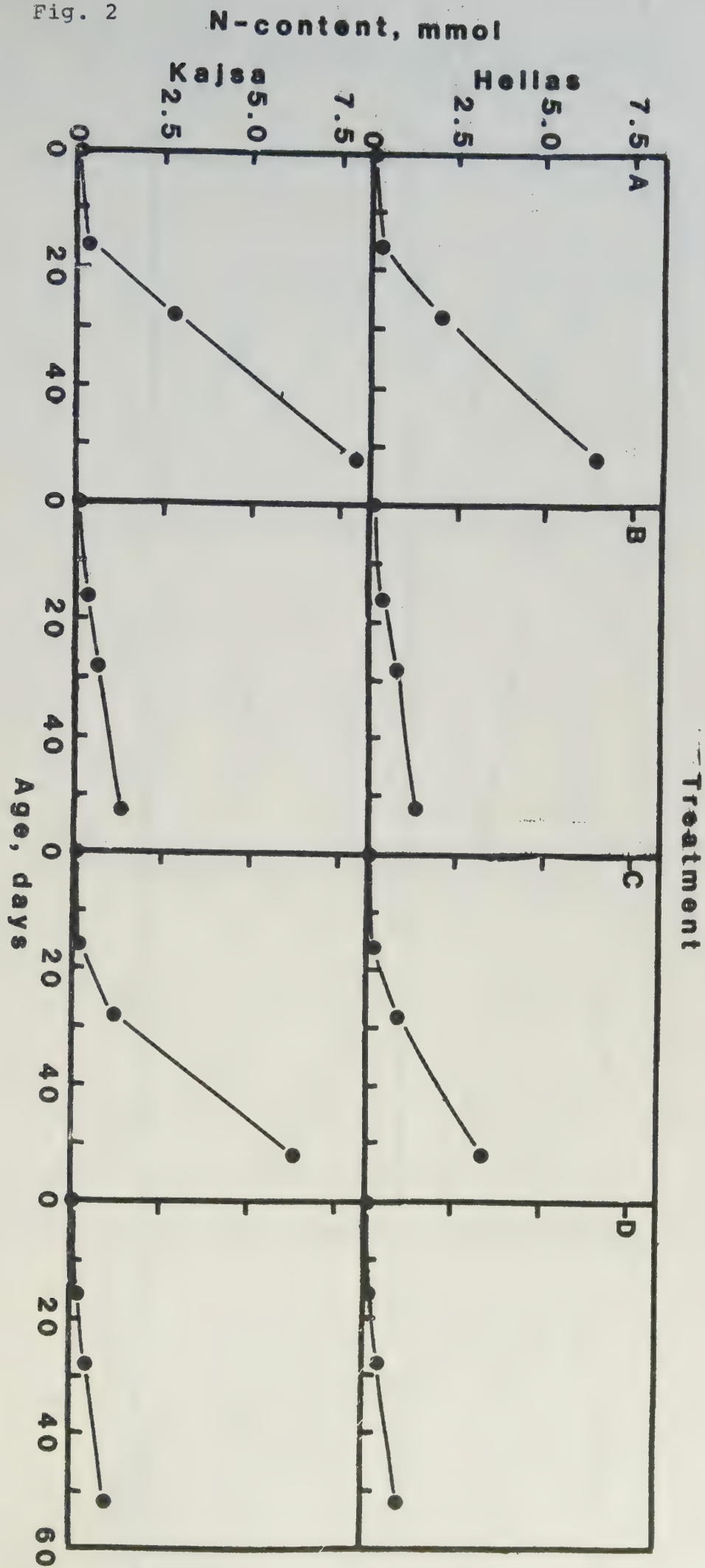


Fig. 3

DW, percentage of total
Kajsa Hellas

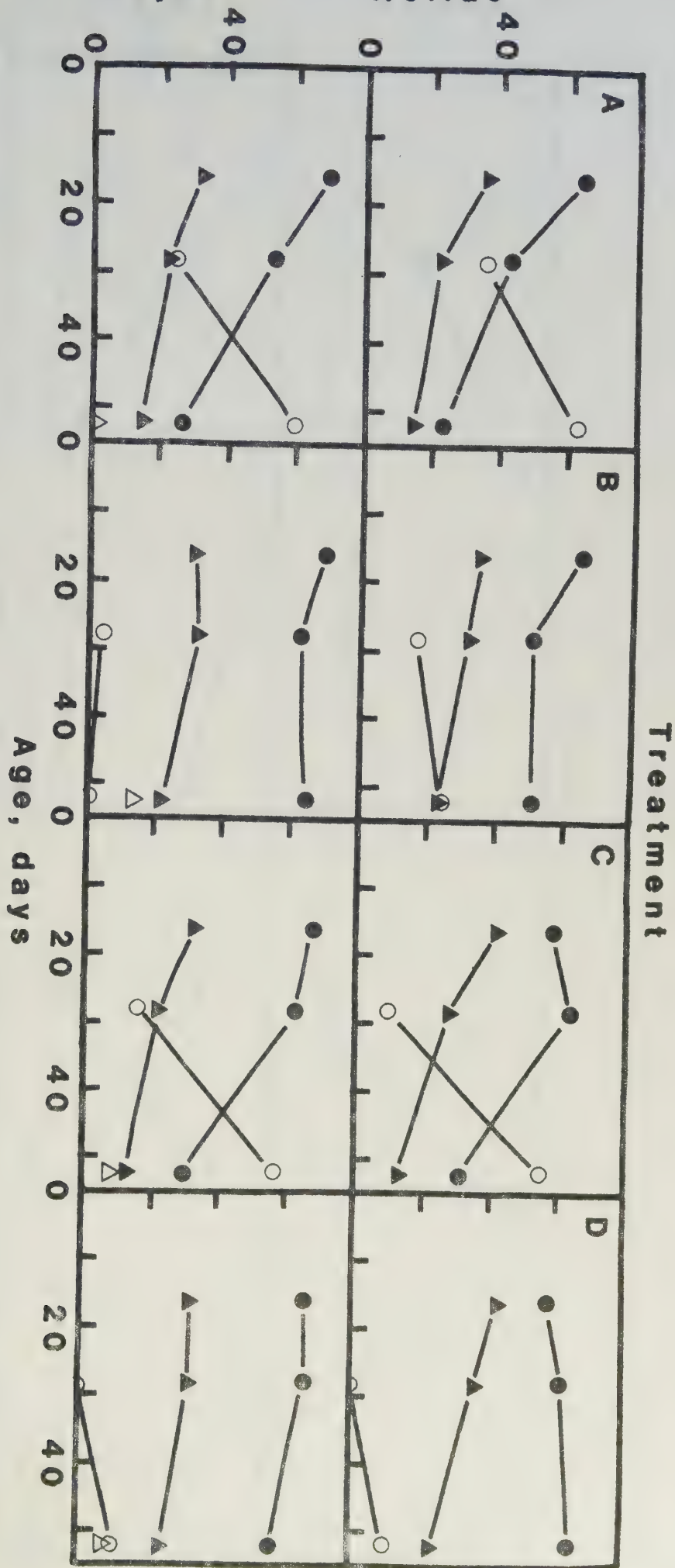


Fig. 4

N-content, percentage of total
Kajsa Hellas

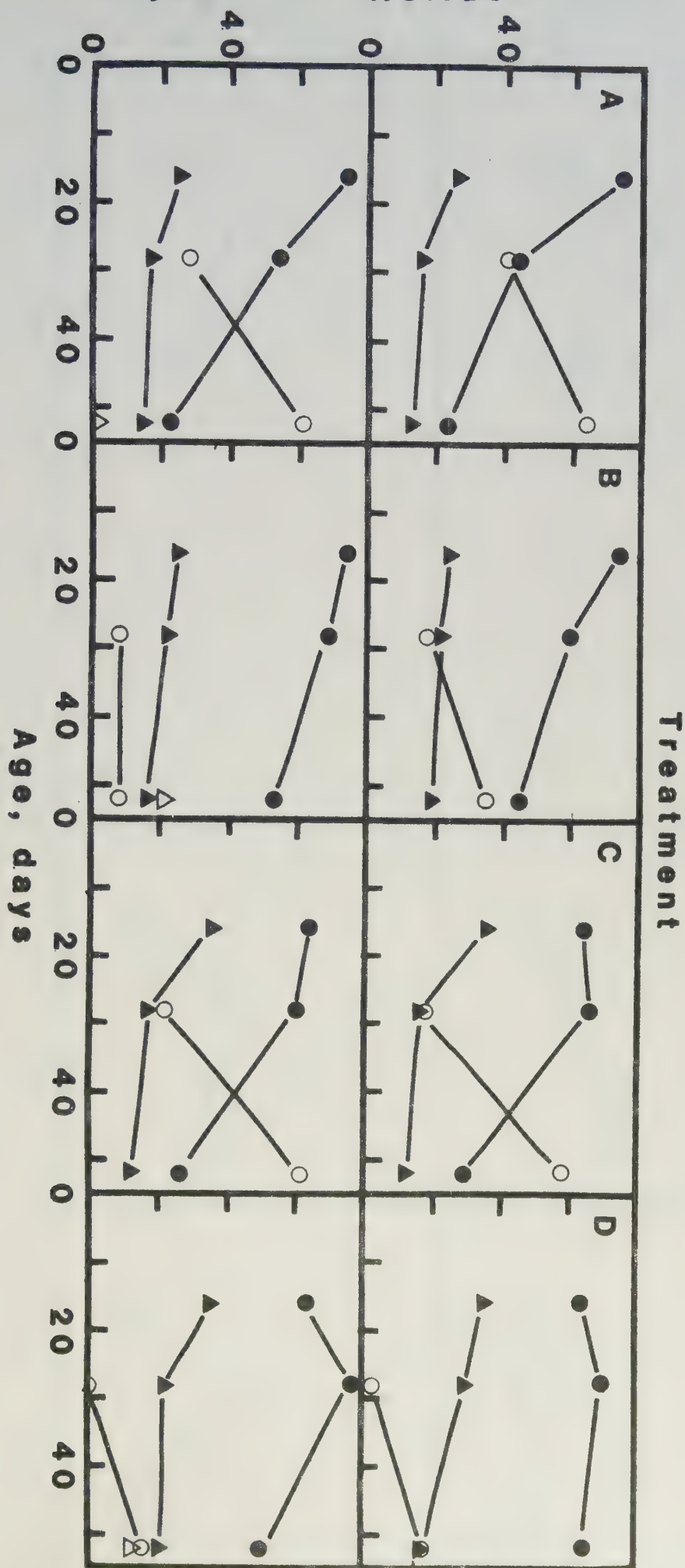
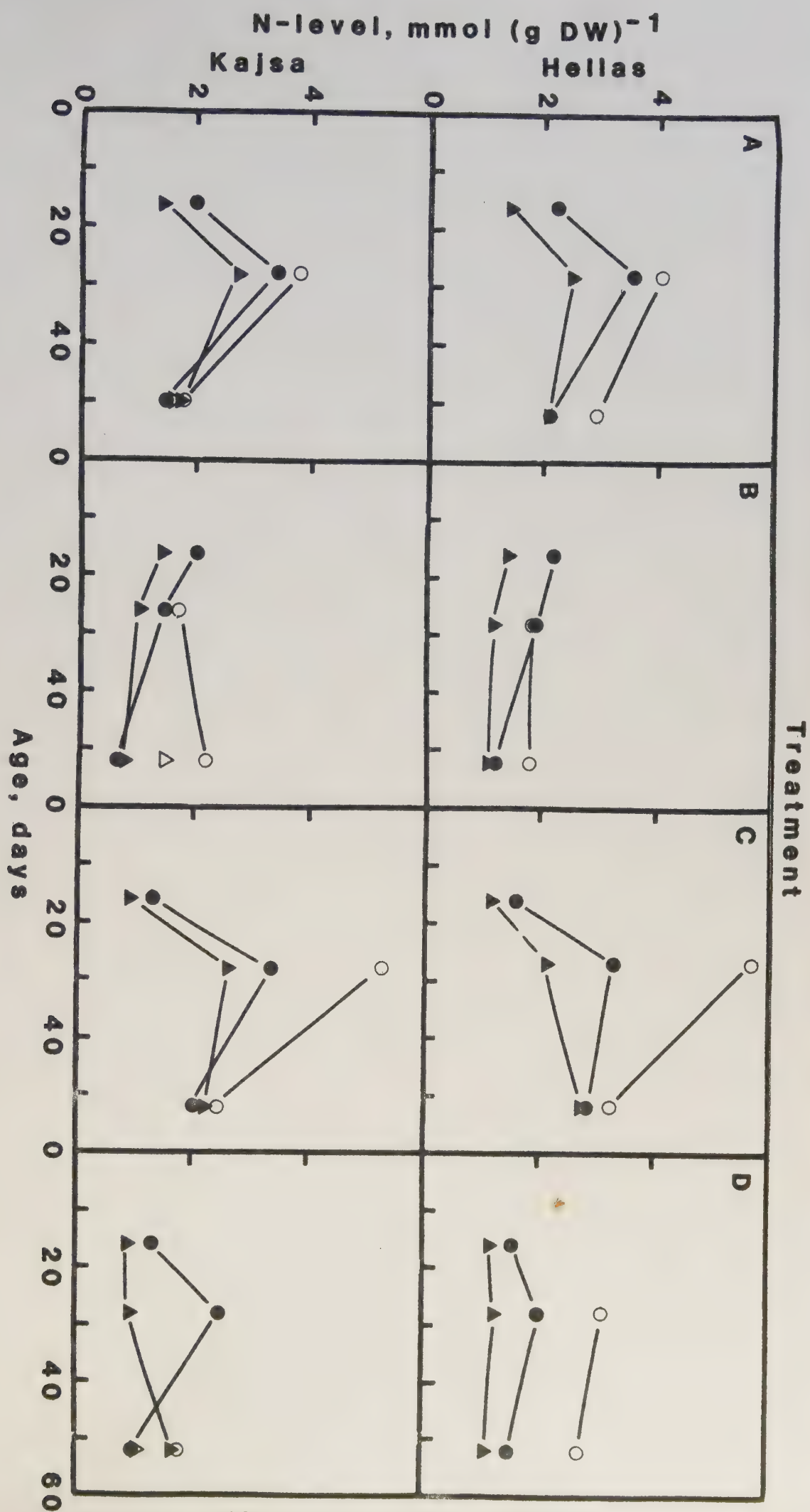


Fig. 5



Preliminary manuscript

Vb. Tiller expansion and net fluxes of nitrogen among main stems, tillers and roots of two barley cultivars

Harald Perby and Paul Jensen

Barley plants (*Hordeum vulgare* L. cvs Hellas and Kajsa), grown in nutrient solutions, were supplied with $^{15}\text{NO}_3^-$ from day 12 to 16. Changes in distribution of ^{15}N between different plant parts were followed during ageing (days 16, 28 and 52) to study differences in redistribution of N induced by variation in NO_3^- supply and choice of cultivar.

Main stems and tillers compete for previously absorbed N and their competitive strength depends on their growth rate. Inhibition of tillering during N stress protects the main stem from detrimental losses of a limiting resource. Tillers on the cultivar Hellas received in most cases proportionally more ^{15}N from the rest of the plant than tillers on Kajsa.

H. Perby and P. Jensen, Dept. of Plant Physiology, Univ. of Lund, P.O. Box 7007, S-220 07 Lund, Sweden.

Introduction

Simpson et al. (1982) proposed a model for N fluxes in a vegetative wheat plant. Since the experiments were done with plants deprived of tillers, they excluded potential sinks for N and carbohydrates (Thorne 1962, Perby and Jensen 1986). Tillers and main stems compete for N. The element is retranslocated from dying tillers to other

plant parts (Williams 1938, Thorne 1962). It is suggested that competition between sinks influences N fluxes in the plants. The emergence of ears - new sinks - changes N fluxes drastically (Simpson et al. 1982, 1983).

In the present experiment, young barley plants of two cultivars were supplied with $^{15}\text{NO}_3^-$. Changes in partitioning of ^{15}N between roots, main stems, tillers and ears were followed during ageing.

Materials and methods

The methods used are described fully by Perby and Jensén (1986). Two groups with three spring barley plants in each (*Hordeum vulgare* L., cvs Hellas and Kajsa) were grown together in 2 l black-painted beakers with 1.8 l medium. The initial NO_3^- concentration in the standard medium was 3.2 mM. Plants were grown at two other NO_3^- concentrations: 10% and 2.5% of the initial NO_3^- concentration of the standard medium. Between days 12 and 16, all plants were supplied with NO_3^- labelled with 99% ^{15}N . The few tillers present on 16-day-old plants were very small. Percentages of ^{15}N in roots, main stems, tillers and ears were determined by optical ^{15}N analysis (Perby and Jensén 1984). Further details are given in Fig. 1 and by Perby and Jensén (1986).

Results

The accumulation of ^{15}N by the plants between day 12 and day 16 is shown in Tab. 1. There was no detectable loss of ^{15}N between day 16 and 52 (data not shown).

In 16-day-old plants, ^{15}N was partitioned similar to

total N (Fig. 1; cf. Fig. 4 in Perby and Jensen 1986). Tillers on 28-day-old plants contained considerable amounts of ^{15}N . For plants initially grown in 10% medium, contents of ^{15}N in main stems decreased between days 16 and 28 (Fig. 1; treatments A and B), while contents of ^{15}N in the roots decreased in Hellas and were constant in Kajsa. The ^{15}N content in the main stems of plants grown in 2.5% medium between day 0 to 16 (C and D) were constant or increased between day 16 and 28. After day 28 there was in five cases of six a net transfer of ^{15}N from main stems to tillers (Tab. 2). The rates of changes in ^{15}N contents in main stems and tillers differed between the cultivars. In five cases out of seven the relative increase in ^{15}N content in the tillers was higher in Hellas. Most roots had a steady state content of ^{15}N after day 28.

Discussion

The simultaneous increase and decrease in ^{15}N content of tillers and main stems, respectively, illustrate the redistribution of N in the vegetative barley plant to expanding tillers (Fig. 1). This may be interpreted along the lines of Pate (1980) and Simpson et al. (1982). Small and rapidly expanding tillers may import carbohydrates and reduced N via the phloem. They receive N also via the xylem, partly as reduced N that has been retranslocated via the roots.

The changes in ^{15}N content in main stems and tillers between days 16 and 28 can be correlated to the distribution of the increases in dry weight (expressed as

increase in dry weight of one plant part in percent of total increase in dry weight) with a significant result. Growth of tillers has a positive effect on ^{15}N content in the tillers ($0.05 > P > 0.01$; Snedecor and Cochran 1974) and a negative effect on ^{15}N content in the main stems ($0.05 > P > 0.01$). Growth of main stems has the opposite effect on partitioning of ^{15}N ($P < 0.01$ for both main stems and tillers). Between days 28 and 52 the trends were the same, but the levels of significance were generally lower, since data from treatment C were lacking. Evidently, main stems and tillers compete for internal N. Their ability to compete is related to their increase in dry weight. By inhibition of tillering, the plants avoid "internal starvation" (Williams 1955) caused by detrimental losses of a limiting resource from the existing parts. A related aspect is that cereal plants change their growth rate by regulation of tillering (Perby and Jensen 1986). They thereby adapt their demand for nutrients to the ambient resources (Helder 1951, Chapin and Bielecki 1982, Chapin 1983).

The relation between demand for minerals and ion uptake is still wrapped in mystery (Clarkson 1984). The content of ^{15}N in the roots of 28- and 52-day-old plants is almost constant. This indicates that considerable fractions of the N retranslocated from sources in the shoots bypass the roots (cf. Simpson et al. 1982, 1983). Alongside phytohormones, the rate of phloem-mediated retranslocation of minerals from the shoots to the roots might be a signal affecting ion uptake by the roots.

The net changes in ^{15}N contents of main stems and tillers differed in general between Hellas and Kajsa (Tab. 2). Except for main stems of 16- to 28-day-old plants grown in the 10% medium after day 16 (treatments B and D), the differences between the cultivars were significant. Tillers on Hellas receive in most cases proportionally more ^{15}N from the rest of the plant than tillers on Kajsa.

The N levels are generally lower in Kajsa (Perby and Jensén 1986) than in Hellas. This difference between the two cultivars may be due to different compartmentation of N (Barneix et al. 1984, Yoneyama and Takeba 1984) and, thus, in amounts of N available for retranslocation.

Acknowledgement

I would like to thank Mr Fredrik Owman and Mr Birger Nilsson for skilful technical assistance. Dr Janet Bornman corrected the language and gave together with Prof. Anders Kylin valuable comments on preliminary versions of the manuscript. The work was supported by grants from O.E. and Edla Johanssons Foundation, The Swedish Society for the Conservation of Nature and the Hierta-Retzius Foundation.

References

- Barneix, A.J., James, D.M., Watson, E.F. & Hewitt, E.J. 1984. Some effects of nitrate abundance and starvation on metabolism and accumulation of nitrogen in barley (*Hordeum vulgare* L. cv Sonja). - *Planta* 162: 469-476.

- Chapin, F.S. 1983. Adaptation of selected trees and grasses to low availability of phosphorus. - *Plant Soil* 72:283-287.
- & Bielecki, R.L. 1982. Mild phosphorus stress in barley and a related low-phosphorus-adapted barley-grass: Phosphorus fractions and phosphate absorption in relation to growth. - *Physiol. Plant.* 54:309-317.
- Clarkson, D.T. 1984. Ionic relations. - In *Advanced Plant Physiology* (M.B. Wilkins, ed.), pp 319-353. Pitman Publishing Limited. ISBN 0-273-01853-1.
- Helder, R.J. 1951. Growth as a determining factor for the intake of anions by maize plants. - *Koninkl. Ned. Akad. Wetenschap.* 54:275-286.
- Pate, J.S. 1980. Transport and partitioning of nitrogenous solutes. - *Annu. Rev. Plant Physiol.* 31:313-340.
- Perby, H. & Jensén, P. 1984. Net uptake and partitioning of nitrogen and potassium in cultivars of barley during ageing. - *Physiol. Plant.* 61:559-565.
- & Jensén, P. 1986. Vegetative adaptation to N stress regimes in two barley cultivars with different N requirement. - *Plant Soil.* (In press).
- Simpson, R.J., Lambers, H. & Dalling M.J. 1982. Translocation of nitrogen in a vegetative wheat plant (*Triticum aestivum*). - *Physiol. Plant.* 56:11-17.
- , Lambers, H. & Dalling, M.J. 1983. Nitrogen redistribution during grain growth in wheat (*Triticum aestivum* L.). IV. Development of a quantitative model of the translocation of nitrogen to the grain. - *Plant Physiol.* 71:7-14.
- Snedecor, G.W. & Cochran, W.G. 1974. *Statistical Met-*

- hods. - The Iowa State University Press, Ames IA. pp. 172-198, 557. ISBN 0-8138-1560-6.
- Thorne, G.N. 1962. Survival of tillers and distribution of dry matter between ear and shoot of barley varieties. - Ann. Bot. 26:37-54.
- Williams, R.F. 1938. Physiological ontogeny in plants and its relation to nutrition. 4. The effect of phosphorus supply on the total-, protein-, and soluble-nitrogen contents, and water content of the leaves and other plant parts. - Aust. J. Exp. Biol. Med. Sci. 16:65-83.
- 1955. Redistribution of mineral elements during development. - Annu. Rev. Plant Physiol. 6:25-42.
- Yoneyama, T. & Takeba, G. 1984. Compartment analysis of nitrogen flows through mature leaves. - Plant Cell Physiol. 25:39-48.

Tab. 1. Accumulation of ^{15}N (given as NO_3^-) during four days (12 to 16) by two cultivars of barley. Values are given as $\mu\text{mol plant}^{-1}$. Data for 16-, 28- and 52-day-old plants were pooled for means of plants supplied with 10% or 2.5% NO_3^- medium between day 0 to 16 (30 and 24 groups, respectively, with three plants in each $\pm$ SD).

Medium	Cultivar	
day 0 - 16	Hellas	Kajsa
10%	77 $\pm$ 10	83 $\pm$ 12
2.5%	23 $\pm$ 2	22 $\pm$ 12

Tab. 2. Changes in contents of ^{15}N in main stems and tillers during ageing. Treatments according to Fig. 1 and Perby and Jensén (1986). H = Hellas, K = Kajsa. Values in percentage total plant content of ^{15}N are based on means for six plant groups with three plants in each. nd = not determined. Cultivar differences : levels of significance (Student's t -test) are indicated by stars: $^{\circ} 0.10 > P > 0.05$ and $** P < 0.01$.

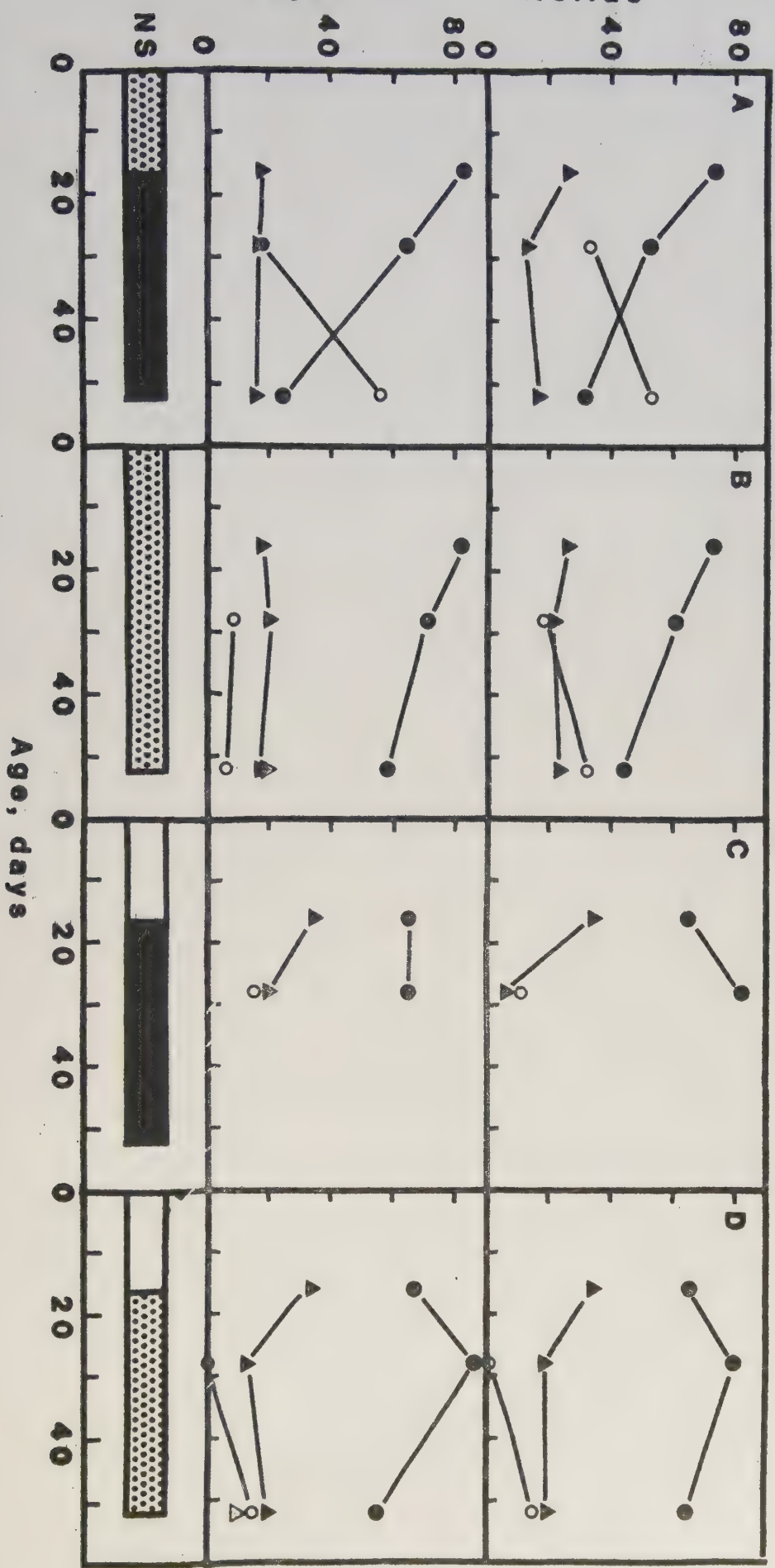
Treat- ment	Culti- var	Days 16 to 28		Days 28 to 52	
		Main stems	Tillers	Main stems	Tillers
A	H	-20 $**$	33 $**$	-23 $**$	20 $**$
	K	-18	18	-40	37
B	H	-12	18 $**$	-17 _o	14 _o
	K	-11	9	-13	-2
C	H	16 $**$	11 $**$	nd	nd
	K	0	15	nd	nd
D	H	15	0.4 $**$	-15 $**$	15 $**$
	K	13	0	-31	2

Figure legend

Fig. 1. Partitioning of ^{15}N in 16-, 28- and 52-day-old barley plants supplied with $^{15}\text{NO}_3^-$ between day 12 to 16. The plants were cultivated with various N-supplies (NS). Standard medium = black area, 10% NO_3^- medium = dotted area and 2.5% NO_3^- medium white area. Filled circles indicate shoots; open circles, tillers; filled triangles, roots and open triangles, ears. Due to dilution by later absorbed N, percentages of ^{15}N in 52-day-old plants initially supplied with 2.5% NO_3^- medium and thereafter standard medium (treatment C) were too low for precise determination. Values are means of six plant groups with three plants in each. SE was usually less than 3% of the mean.

15 N-content, percentage of total
Kajsa Hellas

Fig. 1



Date	Time	Location
1/1/2020	10:00	New York
1/1/2020	11:00	New York
1/1/2020	12:00	New York
1/1/2020	13:00	New York
1/1/2020	14:00	New York

VI. Cultivar differences in nitrate influx among seedlings of barley grown at two different nitrate concentrations

Harald Perby

Influx of $^{15}\text{NO}_3^-$ differed among seedlings of six cultivars of barley (*Hordeum vulgare* L. cvs Alva, Bonus, Cilla, Nürnberg II, Sv 73 608 and Tellus) which were grown in complete nutrient media with either 2 or 10 mM NO_3^- . The cultivar differences in $^{15}\text{NO}_3^-$ influx per root were more prominent than differences in influx per g root fresh weight. For $^{15}\text{NO}_3^-$ influx, the cultivars were ranked in almost the same order after cultivation in media with 2 and 10 mM NO_3^- .

H. Perby, Dept of Plant Physiology, Univ. of Lund,
P.O. Box 7007, S-220 07 Lund, Sweden.

Introduction

Influx and efflux of K^+ and Rb^+ differ among cultivars of barley (Schimansky and Marschner 1971, Pettersson 1978, Glass and Perley 1980, Jensén and Pettersson 1980, Glass et al. 1981, Perby and Jensén 1986). Less attention has been paid to cultivar differences in influx of N compounds. Warncke and Barber (1974) found that the ability to deplete nutrient solutions for NO_3^- differs among plant species and cultivars of corn. Bloom and Chapin (1981) found that influx of NO_3^- and NH_4^+ differed between two cultivars of barley adapted to cultivation

on cold and warm soils. The differences obtained depended on the temperature regime during the uptake experiment. Since NO_3^- influx is strongly influenced by the presence of external NO_3^- (Jackson et al. 1976a,b, Rao and Rains 1976), the question arises whether the NO_3^- supply before an uptake experiment influences differences in NO_3^- influx among cultivars of barley.

In the present experiments, $^{15}\text{NO}_3^-$ influx in seedlings of six cultivars of barley was compared after cultivation in complete nutrient media with two concentrations of NO_3^- .

Materials and methods

Eight plant groups (15 seedlings in each) of each of six cultivars of spring barley (*Hordeum vulgare* L., cvs Alva, Bonus, Cilla, Nürnberg II, Sv 73 608 and Tellus) were prepared as described by Perby and Jensén (1983). Four plant groups were placed together in 2 l black-painted glass beakers with 1.8 l nutrient medium. The 2 mM NO_3^- medium used in the first experiment was composed of: 1.0 mM $\text{Ca}(\text{NO}_3)_2$, 0.5 mM K_2HPO_4 , 1.0 mM KH_2PO_4 , 0.5 mM MgSO_4 , 0.5 mM CaCl_2 , 0.5 mM Na_2SO_4 , 0.03 mM Fe-EDTA, 0.5 μM MnSO_4 , 1.6 μM H_3BO_3 , 3.82 μM ZnCl_2 , 0.32 μM CuCl_2 and 0.21 μM Na_2MoO_4 . pH was ca 6.1.

In the second experiment, the NO_3^- concentration in the medium was increased to 10 mM by addition of 8.0 mM KNO_3 . The plants supplied with medium containing 2mM NO_3^- were germinated and harvested two days before those supplied with 10 mM NO_3^- . Nutrient solutions were continuously aerated and replaced on days 2 and 4, and 10 h

before the start of each uptake experiment. The plants were cultivated in the same climate chamber during the first six days. Thereafter they were transferred to a separate climate chamber in which the uptake experiments were performed. The conditions in both climate chambers were the same as used by Perby and Jensén (1983).

Roots of seven-day-old seedlings were exposed to medium containing 2 mM NO_3^- with 88.7% $^{15}\text{NO}_3^-$ for 1 h, and then to unlabelled medium of the same composition for 10 min. The roots were blotted between filter papers and separated from the shoots. Fresh weights, dry weights, N contents and influx of ^{15}N were determined according to Perby and Jensén (1984) and Jensén and Perby (1986).

Results and discussion

Cultivar differences in dry weight and N content were obtained in both experiments (cf. Perby and Jensén 1983, 1986). Bonus accumulated most and Alva least dry matter and N (Tab. 1).

There was some cultivar variation in NO_3^- influx, mainly in total influx (Tab. 1). For plants grown with 2 mM NO_3^- , influx of $^{15}\text{NO}_3^-$, both totally and per g root fresh weight, could be correlated to the root fresh weight with a significant result ($0.05 > P > 0.01$; Snedecor and Cochran 1974). For plants grown in 10 mM NO_3^- there was no such relationship. Ranking of cultivars according to total NO_3^- influx was almost the same after cultivation in both media. One exception was Nürnberg II, derived from a 19th century German land race (Perby and Jensén 1986). This cultivar was in the highest ranked group

when grown in 2 mM NO_3^- medium, but due to a low influx of NO_3^- per unit root fresh weight, it had the lowest rank when grown in 10 mM NO_3^- medium. The high-yielding cultivar Alva had a low influx of $^{15}\text{NO}_3^-$ per g root fresh weight when grown with in 2 mM NO_3^- , but a somewhat higher rank when grown with 10 mM NO_3^- .

Cultivar differences in root/shoot partitioning of N and recently absorbed ^{15}N were small (Tab. 2; cf. Perby and Jensén 1983). The difference in K^+ -supply (2 or 10 mM) did not induce differences in NO_3^- transport, although K^+ supposedly plays an important role in long-distance transport of NO_3^- (Ben Zioni et al. 1971, Pettersson 1984).

Acknowledgement

I would like to thank Mr Karl-Erik Andersson for skilful technical assistance and Kungliga Fysiografiska Sällskapet for financial support. Dr Janet Bornman corrected the language and gave together with Prof. Anders Kylin and Dr Paul Jensén valuable comments on preliminary versions of the manuscript.

References

- Ben Zioni, A. Vaadia, Y. & Lips, S. H. 1971. Nitrate uptake by roots as regulated by nitrate reduction products of the shoot. - *Physiol. Plant.* 24:288-290.
- Bloom, A.J. & Chapin, F.S. 1981. Differences in steady-state net ammonium and nitrate influx by cold- and warm-adapted barley varieties. - *Plant Physiol.* 68:1064-1067.
- Glass, A.D.M. & Perley, J.E. 1980. Varietal differences

- in potassium uptake by barley. - Plant Physiol. 65:160-164.
- , Siddiqi, M.Y. & Giles, K.I. 1981. Correlations between potassium uptake and hydrogen efflux in barley varieties. A potential screening method for the isolation of nutrient efficient lines. - Plant Physiol. 68:457-459.
- Jackson, W.A., Kwik, K.D. & Volk, R.J. 1976a. Nitrate uptake during recovery from nitrogen deficiency. - Physiol. Plant. 36:174-181.
- , Kwik, K.D., Volk, R.J. & Butz, R.G. 1976b. Nitrate influx and efflux by intact wheat seedlings: Effects of prior nitrate nutrition. - Planta 132:149-156.
- Jensén, P. & Perby, H. 1986. Growth and accumulation of N, K⁺, Ca²⁺ and Mg²⁺ in barley exposed to various nutrient regimes and root/shoot temperatures. - Physiol. Plant. (In press).
- & Pettersson, S. 1980. Varietal variation in uptake and utilization of potassium (rubidium) in high-salt seedlings of barley. - Physiol. Plant. 48:411-415.
- Perby, H. & Jensén, P. 1983. Varietal differences in uptake and utilization of nitrogen and other macro-elements in seedlings of barley, *Hordeum vulgare*. - Physiol. Plant. 58:223-230.
- & Jensén, P. 1984. Net uptake and partitioning of nitrogen and potassium in cultivars of barley during ageing. - Physiol. Plant. 61:559-565.
- & Jensén, P. 1986. Variation in growth and accumulation of N, K⁺, Ca²⁺ and Mg²⁺ among barley cultivars

- exposed to various nutrient regimes and root/shoot temperatures. - *Physiol. Plant.* (In press).
- Pettersson, S. 1978. Varietal differences in rubidium uptake efficiency of barley roots. - *Physiol. Plant.* 44:1-6.
- 1984. Effects of nitrate on influx, efflux and translocation of potassium in young sunflower plants. - *Physiol. Plant.* 61:663-669.
- Rao, K.P. & Rains, D.W. 1976. Nitrate absorption by barley. I. Kinetics and energetics. - *Plant Physiol.* 57:55-58.
- Schimansky, C. & Marschner, H. 1971. Suitability of Rb-86 as a tracer for potassium in studies relating to potassium uptake by maize, sugar beet and four varieties of barley. - *Z. Pflanzenernähr. Bodenkd.* 129: 141-147.
- Snedecor, G.W. & Cochran, W.G. 1974. *Statistical Methods.* - The Iowa State University Press, Ames IA. pp. 172-198, 557. ISBN 0-8138-1560-6.
- Warncke, D.D. & Barber, S.A. 1974. Nitrate uptake effectiveness of four plant species. - *J. Environ. Quality* 3:28-30.

Tab. 1. Dry weights (mg plant⁻¹), total N (mmol plant⁻¹), root fresh weights (g) and ¹⁵NO₃⁻ influx into the roots (umol h⁻¹) of seven-day-old seedlings of six cultivars of barley. Plants were grown in media with 2 or 10 mM NO₃⁻. Values are means of eight groups with 15 plants in each. The cultivars are ranked in classes (small letters, highest rank: a). When the difference is insignificant (P>0.05; Student's t-test), the cultivars are placed in the same class.

Cultivar	DW	N content	Root FW	¹⁵ NO ₃ ⁻ influx (g root FW) ⁻¹ root ⁻¹	
2 mM NO ₃ ⁻					
Alva	75 d	0.25 b	0.33 a,b	3.3 b	1.07 b
Bonus	92 a	0.29 a	0.37 a	5.2 a	1.91 a
Cilla	78 c,d	0.26 a,b	0.32 b	4.2 a,b	1.34 b
Nürnberg II	88 a,b	0.28 a,b	0.36 a,b	5.3 a	1.91 a
Sv. 73 608	83 b,c	0.26 a,b	0.34 a,b	4.9 a	1.64 a,b
Tellus	81 c	0.27 a,b	0.34 a,b	5.0 a	1.71 a
10 mM NO ₃ ⁻					
Alva	76 c	0.25 c	0.30 a	3.2 a,b	0.96 b,c
Bonus	95 a	0.32 a	0.36 a	3.6 a	1.31 a
Cilla	81 b	0.27 b,c	0.33 a	3.0 a	1.01 b
Nürnberg II	86 a,b	0.30 a,b	0.35 a	2.2 b	0.76 c
Sv. 73 608	93 a	0.30 a	0.34 a	3.7 a	1.27 a
Tellus	85 a,b	0.28 a,b,c	0.36 a	3.7 a	1.32 a,b

Tab. 2. Partitioning of N and recently supplied ^{15}N in seven-day-old barley seedlings. Shoot contents are given as means $\pm$ SD for six cultivars. Otherwise as for Tab. 1.

Medium	<u>Shoot content, % of total</u>	
	^{15}N	N
2 mM NO_3^-	54.5 $\pm$ 2.2	80.7 $\pm$ 1.8
10 mM NO_3^-	54.8 $\pm$ 2.7	80.7 $\pm$ 1.2
